Population dynamics of Black-tailed Godwits in the light of heavy metal pollution

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Population dynamics of Black-tailed Godwits in the light of heavy metal pollution

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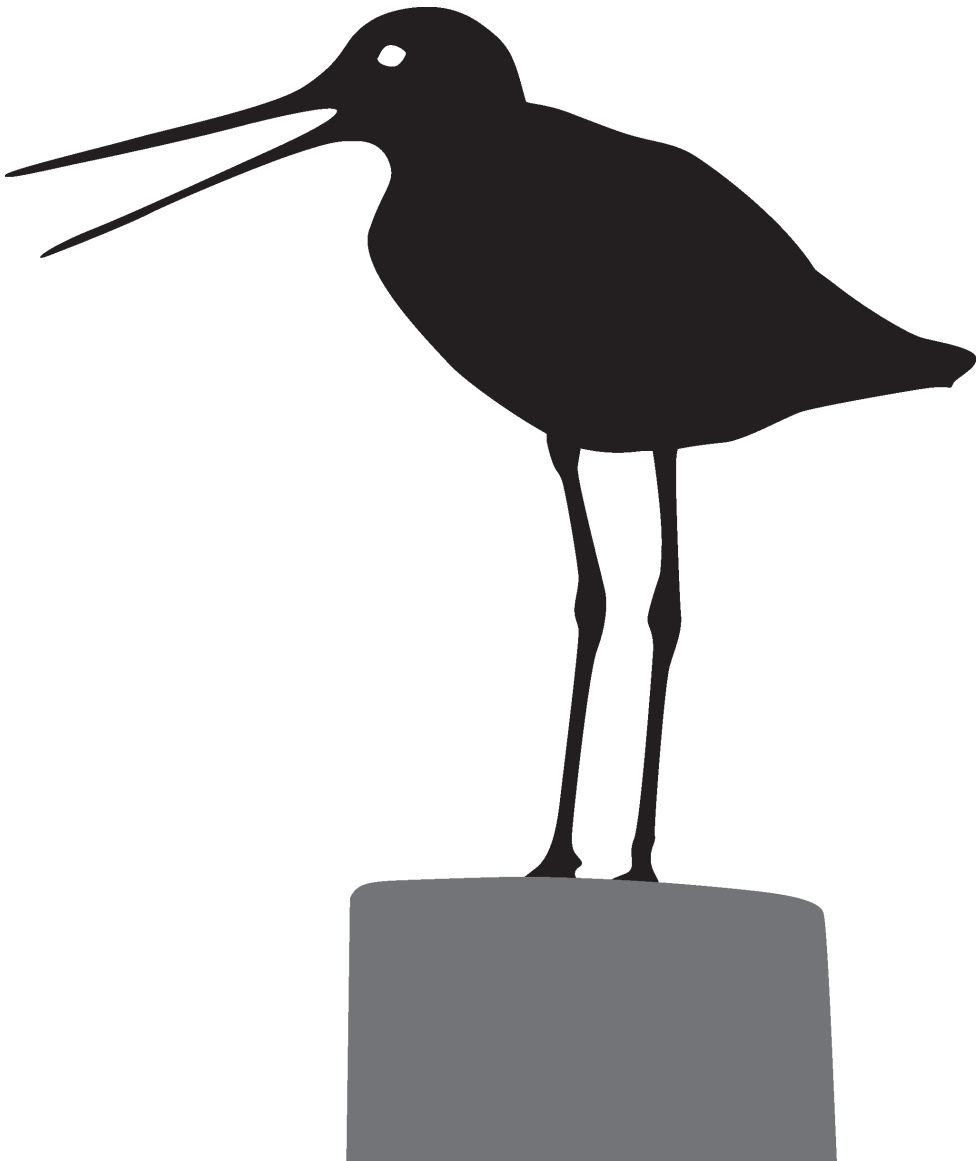
1 Introduction



Project background

The Netherlands is a densely populated and industrialized country. As a result of human activities such as industry, transportation and agriculture, many soils in this country are contaminated (MNP, 2006). Apart from clearly defined sites where pollution is above legislative levels for soil cleanup, many sites in the country are polluted with a mixture of contaminants below such levels (so called diffuse pollution). The Dutch government wanted to know what effect this diffuse pollution has on ecosystems and therefore started the Stimulation Program 'System-oriented Ecotoxicological Research' (SSEO) in 1998, through The Netherlands Organization for Scientific Research (NWO).

Within this program several research projects were initiated that studied the effects of contaminants on different organism groups ranging form bacteria to vertebrates at three selected sites (Zorn, 2004; Vijver, 2005; Notten, 2005; Hobbelen, 2005; Kools, 2006; van der Welle, 2007; Wijnhoven, 2007). The project underlying this thesis was one of them and aimed to determine the effects of mixtures of contaminants on the population dynamics of the Black-tailed Godwit ('grutto' in Dutch). The numbers of Black-tailed Godwits are declining in The Netherlands and the species is classified as vulnerable on the IUCN and the Dutch Red list (see below). As effects on individuals do not necessarily translate directly to populations, impacts of pollutants should be studied at the level of populations (Stark & Banks, 2000).

The following research question was formulated:

"What are the population level effects of diffuse pollution, in the form of heavy metals, on Black-tailed Godwits breeding on contaminated soils in The Netherlands?"

Performing studies on the impact of diffuse pollutants poses several problems. These problems are summarized by van Straalen & van Gestel, (2008): (i) absence of gradients and peak concentrations, as the pollutants are spread out spatially and are not emitted from one point, (ii) absence of good reference sites, (iii) low to moderate concentrations, which may cause small effects that are difficult to measure in the field, (iv) large spatial heterogeneity, which necessitates large sample sizes, (v) mixtures of chemicals from different sources, with possibly interacting effects on biota and (vi) legacies from the past, so that the reference situation is unknown, or local populations may have adapted to the contaminant levels. These authors therefore recommend that effects of diffuse pollution should be analysed by simultaneously considering all possible variables using multivariate models, to be able to separate effects from contaminants from natural variation and other stress factors. However, to do this successfully, a large number of independent study sites is imperative. In species higher up in the food chain such as the Black-tailed Godwit, this is a major problem, because of the large spatial and time scales needed. The

given timeframe of this project only allowed for two sites to be studied. The research described in this thesis was carried out at the contaminated site polder Blokland, and at a non-contaminated reference site, polder Zeevang. The contaminated site lies in "de Ronde Venen", one of the three study sites of the SSEO program. After drainage and peat subsidence, municipal waste from Amsterdam and Utrecht was deposited at this site since the 16th century until 1950, to elevate the land and improve the soil structure and fertility. As a consequence, the top layer of the soil is heterogeneously contaminated with organic pollutants and heavy metals (Lexmond *et al.* 1987). A more detailed description of the two study sites is given in Chapter 2. Being able to compare only two sites, it was difficult to determine the effects of heavy metal pollution on vital rates (demographic parameters determining population growth rate). However, recent data on vital rates were needed for a better understanding of the population decline of this species. Therefore, a second aim of this project was to collect data on reproduction and survival of Black-tailed Godwits, to compare these to data from literature and to develop a population model to diagnose the population dynamics of the species. In this way, we hoped to identify which demographic parameters have declined in the Black-tailed Godwit population, and to determine to which parameters the population growth rate is most sensitive.

Study species

Around 40% of the continental European population of Black-tailed Godwits *Limosa limosa* ssp *limosa* breeds in the Netherlands (BirdLife International, 2004), giving this country a high responsibility in its conservation. Though numbers are declining all over western Europe, threats resulting from habitat deterioration are particularly strong in The Netherlands, being densely populated and one of the leading countries in agricultural intensification (Donald *et al.* 2001). Moreover, the area of grassland has decreased in most European countries in the period 1960-1990, which was most prominent in the Netherlands: 35.6-29.4% of the available habitat was lost (Young *et al.* 2005). Also predation rates of nests and chicks have increased (Schekkerman *et al.* 2009), which amplified recent population declines. Other possible threats to Black-tailed Godwits in The Netherlands are habitat fragmentation, disturbance by traffic and recreation, and pollution.

Not only extrinsic, but also intrinsic factors predispose the Black-tailed Godwit to negative population trends in the light of recent human-induced pressures. Black-tailed Godwits, as other waders, breed on the ground, a trait identified by Van Turnhout *et al.* (2010) as a factor correlating with population declines in Dutch breeding birds. In addition, it is a long-distance migrant, wintering in western Africa. Bohning-Gaese & Bauer (1996) showed for a site in central Europe that populations of both farmland birds and long-distance migrants have declined, in contrast with

Table 1. Reproductive life history traits associated with long-lived animals and associated potential effects on fitness and population dynamics as a result of chronic contaminant exposure (Rowe, 2008).

Trait	Contaminant effects that suboptimize strategy
Large per capita parental investment in offspring	Maternal transfer of high concentrations of contaminants to offspring
Delayed maturation	Mortality before reproduction
	Chronic accumulation of contaminants that may be transferred to offspring upon maturation
	Reduced size at maturity reducing offspring quantity or quality
Iteroparity	Mortality before achieving total potential life long reproductive events
Long embryonic/preparturition/ preweaning period	Chronic exposure of offspring to female-derived contaminants (yolk, placenta, milk)
Long cohort turnover time	Delayed expression of fitness effects at the population level
	Delayed recovery of populations following abatement of fitness effects

more resident species groups and species from other habitats. Moreover, being a habitat specialist, restricted to wet agricultural grasslands and similar natural habitats, the Black-tailed Godwit has little options left when this habitat deteriorates or disappears (Julliard *et al.* 2004; Jiguet *et al.* 2007). Finally, it is a long-lived species (maximum age recorded in literature is 30 years, Zwarts *et al.* 2009), with long pre-adult stage (age at first reproduction usually 2 years, Cramp & Simmons, 1983) and low reproduction rates (one brood per breeding season, with a maximum of four eggs, Cramp & Simmons, 1983), which hinders rapid adaptation to changing environments (Jiguet *et al.* 2007).

Its slow life history strategy also makes the species especially vulnerable to chronic contaminant exposure (table 1, Rowe, 2008). In long-lived species chronic exposure may result in high body burdens through accumulation of the contaminant, which may cause direct effects in adults, such as increased mortality and/or decreased fertility. Alternatively, or additionally, high concentrations of contaminants may be transferred to vulnerable offspring. As the number of offspring in these species is relatively low, this may seriously impair reproductive output. Finally, the long generation times may cause delayed expression of effects of contaminants on the population level, while at the same time delaying recovery rates of populations after removing the contaminant from the environment.

Thesis outline

In **Chapter 2**, concentrations of **heavy metals in soil, earthworms and godwit eggs and feathers** in the polluted and the reference site are compared to see whether elevated concentrations in the soil are transferred to adult godwits via earthworms, their main food item. This could have effects on vital rates of the Black-tailed Godwit population in the polluted site.

In **Chapter 3**, the **reproductive output** of Black-tailed Godwits in the two main study areas is investigated. The timing of reproduction is related to nest success and chick survival and the resulting reproductive output. Possible proximate causes for this relation are discussed. The reproductive output is compared to the minimum reproductive output required for the populations to remain stable and to historical values from literature.

In **Chapter 4**, I focus on **adult survival** in Black-tailed godwits at the two study sites. Adult godwits are captured on the nest, colour ringed and resighted during three years in four different study sites in the Netherlands. Apparent adult survival is estimated with the use of program MARK and compared to historical survival estimates from literature. As permanent emigration cannot be distinguished from mortality in calculations of local survival, a measure for breeding site fidelity in the two main study sites is also calculated, to see if this can help explain differences in apparent survival.

In **Chapter 5**, a visual diagnostic tool is constructed using **matrix models**, to determine under which conditions meadow bird populations are declining, increasing or stable, to be able to estimate missing demographic parameters and to determine the sensitivity of the population growth rate to changes in demographic parameters, despite a value missing.

In **Chapter 6**, literature data on adult and juvenile survival in five meadow waders (Oystercatcher *Haematopus ostralegus*, Lapwing *Vanellus vanellus*, Black-tailed godwit, Curlew *Numenius arquata* and Redshank *Tringa totanus*) are **reviewed** and a statistical **meta analysis** is performed on reproductive parameters collected from different years and sites in Europe, to determine whether survival or reproduction or both have declined in the species concerned.

Finally, the results are collated and discussed in **Chapter 7**, the **general discussion**, by performing an elasticity analysis with a matrix model based on the vital rates estimated at the study sites and by determining which part of the Dutch Black-tailed Godwit population is at risk from heavy metal pollution. Future risks of heavy metal pollution in The Netherlands are discussed and recommendations for conservation of the species are given.

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2 Transfer of heavy metals in the food chain earthworm Black-tailed Godwit: comparison of a polluted and a reference site in The Netherlands

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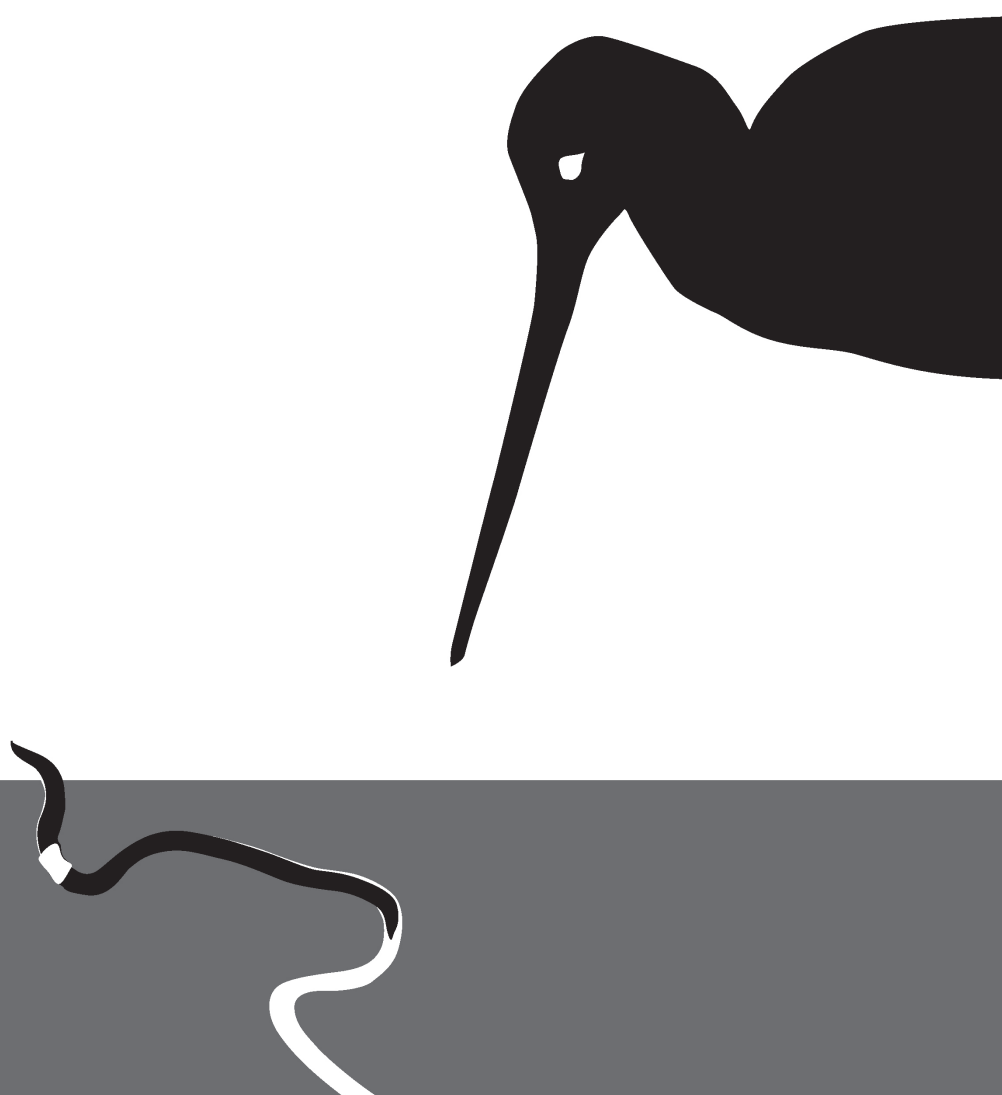

Abstract

The Black-tailed godwit (*Limosa limosa*) is a migratory wader that favours wet meadows for breeding. The species has a Red List status in The Netherlands, as it strongly declined in numbers since the 1960s. Intensification of agriculture and land use change resulting in habitat loss are considered major causes of this decline. In some areas the breeding habitat is contaminated with heavy metals. Adult godwits mainly feed on earthworms in the breeding season, which are known to accumulate heavy metals from the soil. In this paper we investigate the transfer of heavy metals from the soil to the Black-tailed godwit, which may have an additive negative effect on the viability of local populations. We measured heavy metal concentrations in soil, earthworms, and godwit eggs and feathers at a polluted and a reference site. The results suggest that lead, mercury and cadmium are transferred from the soil to godwits even though the species spends only a few months in the breeding area during the year.

Introduction

Many soils in The Netherlands are polluted, often with a mixture of contaminants, resulting in more than 430,000 sites being classified as highly polluted on the basis of soil quality criteria (MNP, 2006). Remediation of all of these sites would require much money and effort. Some of these sites are designated for nature conservation and remediation is questionable since often no adverse effects on ecosystems are apparent. The ministries of Agriculture, Nature conservation and Food quality and of Housing, Land use planning and Environmental management initiated the Stimulation Program System-oriented Ecotoxicological Research through The Netherlands Organization for Scientific Research (NWO), to investigate field effects of contaminant mixtures on ecosystems. In this program, a large number of research groups studied the effects of contaminants on different organism groups at three selected sites. One of these sites, "Ronde Venen", a peat area between Amsterdam and Utrecht (Rutgers, 2008), is strongly but heterogeneously polluted with heavy metals (van Gestel, 2008). Especially Lead, Copper and Mercury levels are, sometimes very locally, above Dutch intervention values and are considered a risk for local ecosystems (Bosveld *et al.* 2000). Klok *et al.* (2006) assessed the effects of heavy metals on earthworms at a polder in this site, polder Blokland, in comparison with a reference site, polder Zeevang, and discussed the consequences for the Black-tailed godwit, a meadow bird which breeds in high densities at both polders and feeds mainly on earthworms during the breeding season. They concluded that the mixture of contaminants at Blokland, mainly heavy metals, reduces growth and maturation of earthworms, thereby reducing population growth rates, which in turn may negatively affect feeding opportunities for Black-tailed godwits.

The Netherlands harbor large breeding populations of Black-tailed godwits, but numbers are declining rapidly (Bird-Life International, 2004) and the species is classified as vulnerable on the Dutch Red List of endangered species. Though it is generally accepted that intensification of agriculture and habitat loss are the main threat to this meadow bird, pollution may have an additive negative effect on local populations. This effect may be indirect by reducing feeding opportunities, as discussed by Klok *et al.* (2006). But Black-tailed godwits may also be affected more directly, by secondary poisoning through feeding on earthworms, which may transfer heavy metals from the soil to their predator.

In this paper we report on the transfer of heavy metals in the food chain earthworm Black-tailed godwit. Given the fact that the Black-tailed godwit is a protected species we used non-invasive techniques to assess heavy metal levels in the species. We measured concentrations of heavy metals in soil, earthworms, and Black-tailed godwit feathers and addled eggs (eggs which did not hatch) at the contaminated site Blokland and the reference site Zeevang.

Material and methods

Research was carried out at a polluted and a reference site in the western part of The Netherlands. The polluted site is situated in polder Blokland (longitude 52°13'N, latitude 4°49'E, ca 180 ha) and the reference site in polder Zeevang (longitude 52°31'N, latitude 4°58'E, ca 130 ha). The polluted site was reclaimed from a wet peat land area by building dykes and lowering the ground water table (Bijlmakers *et al.* 1995). To improve the soil structure and fertility, municipal waste from Amsterdam and Utrecht was deposited there since the 16th century until 1950. As a consequence, the top layer of the soil is contaminated with organic pollutants and heavy metals (Lexmond *et al.* 1987). Especially Lead, Copper and Mercury levels are above Dutch intervention values and are considered a risk for local ecosystems (Bosveld *et al.* 2000).

The reference site resembles the polluted site with respect to soil characteristics and management. Both polders originate from peaty marshlands and are managed as intensively and extensively used grasslands mown for silage or grazed by dairy cattle and sheep. They are important breeding areas for meadow birds, mainly Lapwings (*Vanellus vanellus*), Black-tailed godwits, Redshanks (*Tringa totanus*), and Oystercatchers (*Haematopus ostralegus*). The sites are chosen wide apart (approximately 40 km) to reduce the probability that godwits breeding at one site feed at the other.

At the polluted and the reference site eight locations were chosen with clusters of nests of Black-tailed godwits in 2002. In March 2003 and 2004 six randomly chosen soil samples were taken within 100 m from each location centre, to remain well within the feeding range of the breeding godwits (1-12 ha, unpubl. data). Soil samples (20 x 20 cm and 10 cm deep) were dug with a spade and transported to the laboratory. Soil fauna in the samples was collected by hand sorting and divided into earthworms and other invertebrate species. Earthworms were measured, weighed and classified to the species level (Sims *et al.* 1985). For further analysis of soils and earthworms the six samples per location were pooled.

During the breeding season from March until half June in 2002 and 2004 both study areas were searched for nests of the Black tailed Godwit and the nests were monitored until the eggs hatched or the nest failed. Breeding godwits were trapped on their nest, in 11 cases using a kidney shaped walk-in trap and in all other cases using a trap with a spring that is triggered by the bird. From each wing the second and third tertials were collected as these are heavier than body feathers and dispensable during flight. We used the same feathers for each bird to avoid difficulties in comparability due to differences in moulting pattern, pigmentation and external contamination.

Addled eggs were collected and stored in a refrigerator. Sample sizes are given in Table 1.

Table 1. Numbers of samples collected for heavy metal analyses in 2002-2004 in a polluted (Blokland) and reference site (Zeevang) in The Netherlands.

year	Soil		Earthworms		Eggs (nests)		Feather samples (= no. godwits)	
	Blokland	Zeevang	Blokland	Zeevang	Blokland	Zeevang	Blokland	Zeevang
2002	-	-	-	-	19 (9)	11 (5)	12	16
2003	8	8	8	8	-	-	-	-
2004	8	8	8	8	12 (6)	25 (15)	12	16
Total	16	16	16	16	31 (15)	36 (20)	24	32

All analyses were performed according to standard operational procedures (SOPs) from Alterra. Egg contents and earthworm samples were freeze-dried and soil samples were dried at 40°C. Egg contents and soil samples were homogenised before digestion. Of soil, earthworms and eggs 2g and of feathers 0.1g was digested with HCl and HNO_3. The destruates were analysed for heavy metals using atomic emission spectrometry (ICP-AES). In egg contents and feather samples collected in 2002 and 2004 some heavy metals, namely Cadmium, Chromium, Copper, Nickel, and Lead, were analysed using mass spectrometry (ICP-MS), which is more sensitive (can detect lower concentrations) than ICP-AES. Mercury concentrations were measured using the cold vapour technique (atomic absorbency spectrometry, ICP-AAS).

Heavy metal concentrations were log-transformed and tested for differences between sites using Analysis of Variance (ANOVA, with an unbalanced treatment structure when sample sizes were unequal), correcting for differences between years in Genstat (Genstat 5 Committee, 1987). Some metal concentrations in eggs and feathers were below the detection limit. In such cases a new value was calculated by multiplying these limits by 0.5 and by a factor correcting for the amount of sample analysed. Data on eggs from the same nest were pooled.

Results

Concentrations of Copper, Mercury, Lead and Zinc were significantly higher in soil samples collected in Blokland compared to Zeevang ($p<0.001$, Table 2), while the concentrations of Chromium were significantly lower ($p<0.001$).

Earthworm samples collected at the two sites mainly consisted of three species: *Allolobophora chlorotica*, *Aporrectodea caliginosa* and *Lumbricus rubellus*. Mean earthworm densities in the upper 10 cm of soil varied between 421 earthworms/m² and 594 earthworms/m² and biomass between 90.1 g/m² and 125.9 g/m² (Table 3) and did not differ significantly between sites or years (density: $p = 0.516$, biomass: $p = 0.513$).

Table 2. Concentrations of heavy metals in soil and earthworm samples, egg contents and feathers of Black-tailed godwits from a polluted (Blokland) and a reference site (Zeevang) in The Netherlands.

	Soil (2003+2004)			Earthworms (2003+2004)			Eggs (nests, 2002+2004)			Feathers (2002+2004)		
Heavy metal	Blokland (n = 16)	Zeevang (n = 16)	p	Blokland (n = 16)	Zeevang (n = 16)	p	Blokland (n = 15 nests = 31 eggs)	Zeevang (n = 20 nests = 36 eggs)	p	Blokland (n = 24 godwits)	Zeevang (n = 32 godwits)	p
Cd	0.93 (0.66-1.39)	0.88 (0.56-1.16)	0.214	4.27 (2.11-6.32)	3.07 (1.65-4.61)	<0.001	-	-	-	0.07 (nd-0.19)2	0.02 (nd-0.24)2	<0.001
Cr	35.06 (29.92-41.43)	43.85 (33.30-49.93)	<0.001	1.94 (nd-13.16)	3.19 (1.19-11.93)	0.181	1.10 (0.44-3.69)	1.60 (0.58-9.96)	0.966	3.38 (0.68-23.66)	0.97 (nd-12.30)2	0.002
Cu	77.63 (54.16-106.08)	29.65 (22.15-36.71)	<0.001	15.35 (11.18-25.52)	9.12 (6.68-11.62)	<0.001	3.55 (2.58-5.06)	3.56 (2.89-5.16)	0.026	14.93 (7.53-35.89)	16.00 (8.78-38.82)	0.471
Hg	1.77 (0.97-3.01)	0.35 (0.29-0.50)	<0.001	1.06 (0.28-1.80)	0.30 (0.16-0.51)	<0.001	0.33 (0.16-0.67	0.21 (0.13-0.41)	0.040	0.52 (nd-2.22)2	0.52 (0.12-1.83)	0.992
Ni	23.12 (18.17-28.34)	22.75 (17.74-25.83)	0.655	2.14 (0.73-8.73	2.39 (0.75-7.59)	0.517	0.25 (0.03-1.64)1	0.49 (0.02-4.61)1	0.938	0.73 (nd-14.22)2	0.36 (nd-33.11)2	0.154
Pb	335.74 (162.53-763.61)	92.47 (75.30-149.43)	<0.001	35.24 (13.73-105.85)	6.10 (2.20-15.81)	<0.001	0.17 (nd-0.51)1	0.02 (nd-1.04)1	0.024	2.79 (0.73-10.81)	1.66 (0.49-10.23)	0.003
Zn	185.35 (129.59-303.90)	123.03 (101.49-139.79)	<0.001	508.16 (320.95-779.41)	415.91 (217.23-650.51)	0.003	54.70 (43.15-69.50)	56.11 (47.21-67.30)	0.113	207.97 (123.31-545.76)	205.12 (133.97-567.55)	0.897

Year was included as a random factor in the statistical models. Geometric mean and range in brackets (mg/kg dry weight). nd = not detectable.

[1] *Nickel concentrations were below detection limit in 4 eggs, 2 from Blokland and 2 from Zeevang, and Lead concentrations in 12 eggs, 2 from Blokland and 10 from Zeevang.*

[2] *In feathers concentrations of Cadmium were below detection limit in 16 godwits, 2 from Blokland and 14 from Zeevang, of Chromium in 8 godwits, all from Zeevang, of Mercury in 1 godwit from Blokland, of Nickel in 12 godwits, 4 from Blokland and 8 from Zeevang.*

In earthworms collected in Blokland, levels of Cadmium, Copper, Mercury, Lead and Zinc, were elevated compared to those collected in Zeevang ($p<0.005$, Table 2).

In total, 67 addled eggs were collected from 35 different nests (Blokland: 31 eggs from 15 nests, Zeevang: 36 eggs from 20 nests, Table 1).

In most eggs Cadmium concentrations were below the detection limit and Cadmium was therefore excluded from the statistical analyses of egg data. Copper, Mercury and Lead differed significantly between sites, with higher levels of Mercury and Lead in Blokland ($p<0.05$, Table 2) and higher levels for Copper in Zeevang ($p<0.05$).

Feathers of 24 godwits were collected in Blokland and of 32 in Zeevang (Table 1), with a mean sample weight of 0.129 g. Cadmium, Chromium and Lead concentrations were higher in feathers from birds breeding in Blokland than from those breeding in Zeevang ($p<0.005$, Table 2).

Discussion

Measured soil concentrations were all below Dutch intervention values, but Copper, Mercury, Lead and Zinc in Blokland were above target values indicating slightly contaminated soils. Concentrations of Mercury in Zeevang only just exceeded target values by 0.005 mg/kg (Table 4).

Cadmium was not significantly elevated in the soils from the polluted site, however concentrations were significantly higher in earthworms at this site, suggesting higher soil levels at the polluted site than at the reference site. Earthworms are known to strongly accumulate Cadmium (Ma, 1982), which may amplify differences in Cadmium level between the sites, that were not statistically significant in soils. Cadmium was also higher in feathers collected at the polluted site, suggesting transfer of this metal in the food chain. Also Lead seems to be transferred from soil to godwits, its concentrations being significantly elevated in soils, earthworms, eggs and feathers. Transfer of Lead has also been found for the food chain earthworm Blackbird (*Turdus merula*) by Scheifler *et al.* (2006) at Lead levels in earthworms which were an order of magnitude lower than the levels found in this study.

Heavy metal contents of feathers and eggs of Black-tailed godwits have not been studied previously. Concentrations of all heavy metals in eggs at the two study sites were generally comparable to or even below literature values for other bird species (Herring gulls (*Larus argenatatus*): Gochfeld, 1997, Merlin (*Falco columbarius*): Newton *et al.* 1999, *Ciconiiformes* Hernandez *et al.* 1987, Common loon (*Gavia immer*): Evers *et al.* 2003), though only few data could be found for Chromium. Cadmium is considered not to be efficiently transferred from female to egg in some birds (Sell, 1975) and concentrations in eggs are therefore generally low (Burger *et al.* 1991, Gochfeld, 1997, Mora, 2003). This also seems to be the case in the Black-tailed godwit, as nearly all Cadmium concentrations in eggs were below the detection

Table 3. Earthworm densities and biomass in a polluted (Blokland) and reference site (Zeevang) in The Netherlands.

Site	Measure	2003	2004
Blokland	Density (/m2)	568 ± 174 (8)	421 ± 318 (8)
	Biomass (g/m2)	90.1 ± 33.5 (8)	125.9 ± 77.3 (8)
Zeevang	Density (/m2)	594 ± 204 (8)	496 ± 144 (8)
	Biomass (g/m2)	124.8 ± 34.9 (8)	114.9 ± 43.5 (8)

Mean (based on density or biomass in upper 10 cm of soil) ± SD, sample size in brackets.

Table 4. Target and intervention values for the soil at the contaminated (Blokland) and reference (Zeevang) site.

Heavy metal	Standard soil (10% OM, 25% clay)		Blokland (25% OM, 23.7% clay[1])		Zeevang (34.4% OM, 24.8% clay[1])	
	Target value	Intervention value	Target value	Intervention value	Target value	Intervention value
Cd	0.8	12.0	1.1	16.7	1.3	19.8
Cr	100.0	380.0	97.4	370.1	99.6	378.5
Cu	36.0	190.0	44.2	233.4	50.5	266.6
Hg	0.3	10.0	0.3	10.7	0.3	11.4
Pb	85.0	530.0	98.7	615.4	109.2	680.9
Ni	35.0	210.0	33.7	202.2	34.8	208.8
Zn	140.0	720.0	158.6	815.7	176.0	905.1

Values for standard soil (Swartjes, 1999) have been adjusted for organic matter and clay contents of the soil at the study sites (Directoraat Generaal Milieubeheer, 2000). All values given in mg/kg dry weight.

[1] *Klok et al. 2006*

limit. Concentrations of Mercury and Lead were elevated in godwit eggs from the contaminated site as compared to the reference site. Copper, however, was lower in eggs from the contaminated site as compared to the reference site, while being elevated in both soil and earthworm samples from the contaminated site. This might partly be explained by the fact that Copper, like Zinc, is an essential element that is regulated by organisms (Pascoe *et al.* 1996). Therefore concentrations in organisms are not necessarily linked to soil concentrations. However, this does not explain why levels in eggs were higher at the reference site.

Concentrations of heavy metals in feathers were low to intermediate compared to literature on other species, except for Copper and Zinc, which seem somewhat higher (Burger, 1993, Dauwe *et al.* 2003, Burger *et al.* 1999). As these concentrations do not differ between the two sites and the uptake of both metals is regulated, these values are probably species specific.

Scheifler *et al.* (2006) point out that comparison of literature on heavy metal concentrations in feathers faces some problems, as feather concentrations depend on the type of feather (concentrations may show large differences resulting from moulting pattern (Furness *et al.* 1986) and pigmentation (Dmowski *et al.* 1984 in Dauwe *et al.* 2003)) and external contamination (Dauwe *et al.* 2003).

The Black-tailed godwit is a migratory species and spends only 4-5 months at the study sites during the breeding season. Individuals winter in Western Africa and pass through Western Europe during migration. If godwits from Zeevang and Blokland follow the same migration route and winter at the same site, any differences in heavy metal burdens can be explained by differences in heavy metal concentrations at the breeding sites. However, if this is not the case, the heavy metals may well originate from elsewhere. Unfortunately, we do not have enough data on migration routes, let alone winter sites, to exclude additional effects from other than breeding sites. In the Icelandic subspecies for example, individuals that occupy higher quality breeding sites, also use higher quality winter sites (Gunnarsson *et al.* 2005). Breeding and winter sites may therefore be linked and more data on staging and winter sites are needed to draw unambiguous conclusions.

Heavy metals can be sequestered in the feathers during the short period of feather growth and thus reflect the blood concentration at this period (Dauwe *et al.* 2003). During moulting birds are able to eliminate substantial amounts of some heavy metals (Burger, 1993). Therefore we chose to study feathers which are usually formed during or just after the breeding period. Most of the collected tertials (89%) belonged to the non-breeding plumage, which is usually formed during or after breeding on the breeding grounds and staging sites, though the post breeding moult may be interrupted and continued at the wintering sites (Van Dijk, 1980). Feathers are, however, not the single structures in which heavy metals are stored, such that blood concentrations at the time of feather formation may both reflect historic and current exposure. Therefore, even by choosing those feathers that are formed at the breeding site historic exposure cannot be ruled out. A way to learn more about the origin of the reserves from which the feathers have been formed, would be to use stable isotopes. Klaassen *et al.* (2001) used this technique to show that waders are income breeders, meaning that they prepare their eggs from recently ingested nutrients. This might indicate that heavy metal levels found in godwit eggs reflect pollution levels at the breeding grounds, though it remains unknown whether these metals follow the same distribution pattern within the body as do nutrients.

Conclusions

The Black-tailed godwit is a long-lived species (maximum age observed in The Netherlands > 17 years, Beintema *et al.* 1995) with high nest site fidelity. In Blokland the median distance between nests in successive years was 252 m (Roodbergen *et al.* 2008). This implies that although possible transfer of heavy metals from the breeding site is restricted to a relatively short breeding season, it may extend over a large period of the adult life of an individual. The fact that some heavy metals were significantly higher in soils, earthworms, eggs and/or feathers strongly suggests transport of these heavy metals from earthworms at the breeding site to Black-tailed godwits. We can, however, not be certain to what level heavy metals in wintering and migratory sites added to the measured concentrations in feathers and eggs.

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3 Timing of breeding and reproductive output in two Black-tailed Godwit populations in The Netherlands

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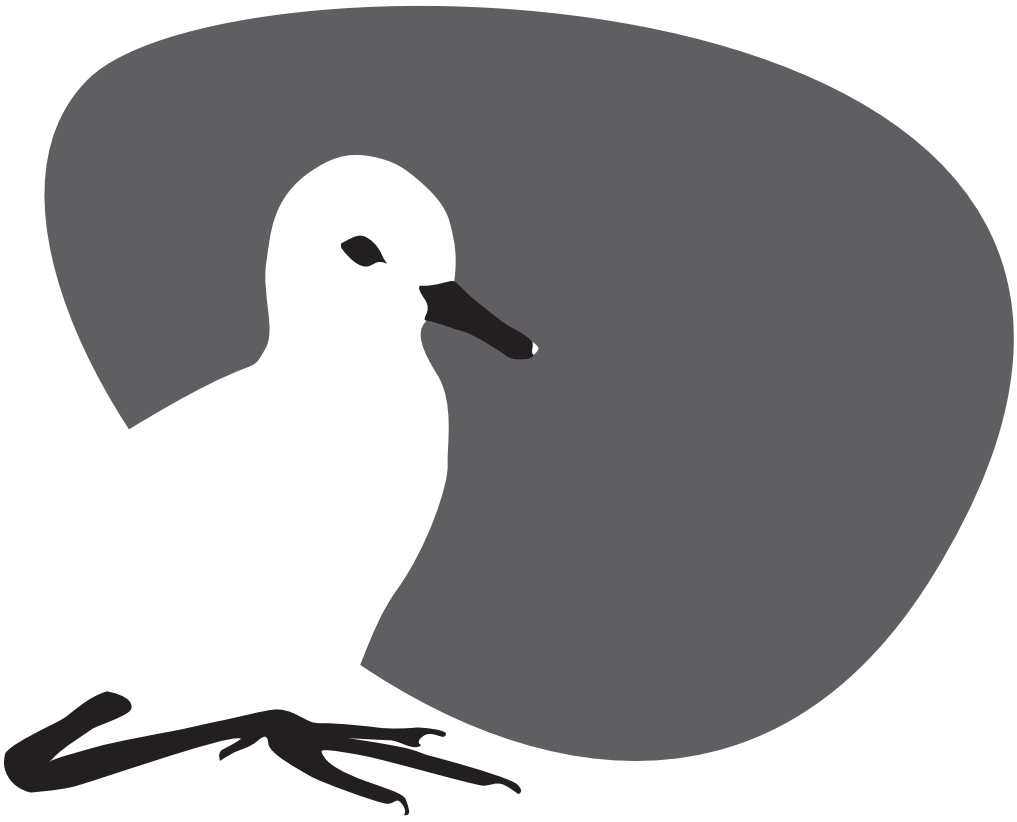

Abstract

To get a better understanding of the current population decline of Black-tailed Godwits in The Netherlands, we determined reproductive parameters in two Dutch breeding populations over the period 2002–2005 and investigated the relationship between reproductive output and timing of breeding. Annual median laying dates ranged from 14 to 25 April, and median hatching dates from 11 to 28 May. Sites differed in laying dates but not in hatching dates. Daily survival rate of nests was positively correlated to nest age and was affected by year and by the interaction of year and site, but not by laying date. The number of eggs hatching per successful nest also did not depend on laying date. Maximum chick survival (maximum estimate of the number of chicks fledged divided by the number of chicks hatched from the nest) and the probability of raising at least one chick to fledging declined significantly with hatching date, resulting in a decline of reproductive output with laying date. Minimum chick survival correlated negatively with cumulative minimum temperature during the first week after hatching. Duration of rainfall during the chick-raising period did not affect chick survival. Our estimates of reproductive output were lower than found in previous studies, and in most years reproductive output was too low to compensate for adult and juvenile mortality. Five possible proximate causes for the seasonal decline in chick survival are discussed: parental quality, weather conditions, food availability, predation pressure and mowing of the grassland habitat.

Introduction

The Black-tailed Godwit *Limosa l. limosa* is a long-distance migrant breeding in European agricultural grasslands and wintering in western Africa. Around 40% of the population breeds in The Netherlands. As in most meadow birds, breeding numbers have rapidly declined all over Western Europe during the last 40 years (BirdLife International 2004). Insufficient reproduction is generally assumed to have caused the population decline (Kruk *et al.* 1997, Schekkerman & Müskens 2000, Ratcliffe *et al.* 2005, Schekkerman *et al.* 2005). Survival prospects seem to have played only a minor role in the decline as adult survival rates have remained stable in The Netherlands over the past decades (Roodbergen *et al.* 2008).

Timing of breeding is an important factor in the breeding ecology of birds in seasonal environments (Brinkhof *et al.* 1997, Both & Visser 2001) as the period of maximum food requirements of chicks must coincide with maximum food availability (e.g. Högstedt 1974, Newton & Marquiss 1984, Visser *et al.* 1998). Proximate factors for a proper timing are the food available to females before egg laying or weather conditions early in the season. In bird species as Great Tit *Parus major* and Pied flycatcher *Ficedula hypoleuca* climate change caused a mismatch between timing of breeding and optimal conditions for reproduction (Visser *et al.* 1998, Both & Visser 2001). In agricultural landscapes, birds face human-induced factors due to changes in land management, which may change even more rapidly than natural factors. Beintema *et al.* (1985) showed that mean hatching dates of chicks, as calculated from ringing data, had advanced by two weeks from 1911 to 1974 in six meadow bird species, amongst them the Lapwing *Vanellus vanellus* and Black-tailed Godwit. They considered this advance a result of a similar advance in mowing dates and/or in seasonal food availability for adults due to increased use of fertilizers. Both *et al.* (2005), however, argued that climate change, not agricultural intensification, caused laying dates to advance in Lapwing over the period 1901–2003. Whatever the underlying cause, a change in laying dates may lead to a mismatch between the timing of breeding and the optimal window for rearing young in meadow birds.

In this paper we investigate the relationship between the reproductive output of two Dutch breeding populations of Black-tailed Godwits and the timing of breeding. Considering the changes in management practices and in climatic conditions, it is possible that the timing of breeding is no longer matched to optimal conditions for reproduction, or even that conditions are never good enough for sufficient reproduction. We monitored two colour-ringed breeding populations over four years and assessed breeding pair densities, laying and hatching date, nest and chick survival and overall reproductive output.

Methods

Study areas

Fieldwork was carried out at two sites in the western part of The Netherlands: Polder Blokland (52°13'N, 4°49'E, province of Utrecht, c. 180 ha) and Polder Zeevang (52°31'N, 4°58'E, province of Noord-Holland, c. 130 ha). The two sites are similar in soil characteristics and agricultural management. Both polders originate from peaty marshlands and therefore mainly consist of peat soils, and are a mixture of intensively and extensively used grasslands, either mown for silage or grazed by dairy cattle and sheep. In both sites roughly one third of the area is under management agreements, some aiming to protect meadow birds (i.e. birds breeding in agricultural grasslands) and some to increase plant diversity. The agreements directed at meadow birds usually restrict farming activities, by e.g. delaying mowing dates and leaving patches unmown for the chicks to hide in, and protect nests during these activities. Both sites hold high numbers of breeding meadow birds, mainly Black-tailed Godwits, Lapwings, Redshanks *Tringa totanus* and Oystercatchers *Haematopus ostralegus*. A more detailed description of the study sites can be found in Roodbergen *et al.* (2008).

Data collection

During the study period, we measured breeding pair densities (2003–2005), laying and hatching date, nest success, proportion of eggs hatched per successful nest (2002–2005) and chick survival (2002–2004). The frequency of field visits was 5–6 days per week during the peak of the breeding season (4 days per week in 2005). In Zeevang more volunteers searched for nests and the grass started growing later in the season than in Blokland, which made it easier to find nests and to observe colour-ringed godwits.

Breeding pair densities

The number of breeding territories was estimated using standardized territory mapping (Teunissen & van Kleunen 2000). From April to June, three mapping censuses were made and a breeding territory was assigned if a pair or a male was present on the territory during at least two visits, of which at least one in the period from 10 April to 10 May. Because individual birds can easily be missed during observations, in addition to the territory mapping the number of nests was counted as a proxy for breeding pair density.

Nests and laying dates

The study areas were searched for nests by volunteers and MR. Nests found were marked with a bamboo stick at a distance of 2 m and checked at least once a week. A GPS was used to determine their coordinates. If the clutch was complete when

found, i.e. containing four eggs, the laying date was estimated by floating two eggs in an incubometer (van Paassen *et al.* 1984). If the clutch was still incomplete (< 4 eggs) the laying date could be estimated more precisely, as usually one egg is laid per day (Cramp & Simmons 1983). For those statistical analyses in which laying date was included only clutches found incomplete and freshly completed (≤ 2 days old) were used, to avoid possible errors of the estimate for laying date. In Black-tailed Godwits, the incubation time is c. 23 days and all eggs hatch within one or two days (Cramp & Simmons 1983). At each successful nest the number of eggs hatched was determined by checking for remaining unhatched eggs.

Chick survival

As godwit chicks leave the nest soon after hatching and seek food and shelter in tall vegetation, they are difficult to observe. In contrast, adults tending chicks are very conspicuous and chick survival can be estimated by following broods of which at least one of the parents is individually marked. Adult godwits were captured on the nest (Roodbergen *et al.* 2008), measured, weighed and provided with an individual combination of Darvic colour rings and a metal ring with an individual number. In all cases but five, capture attempts were ceased after capture of one of the partners. The sex was determined from biometry and plumage characteristics (Schroeder *et al.* 2008).

In addition to colour ringing, in 2003 and 2004 most of the godwits caught were equipped with a radio-transmitter, making it easier to locate the family during the chick-rearing period. Transmitters weighed c. 3 g and emitted a signal at a specific frequency around 153 MHz, which could be received up to a distance of a few hundred metres when in tall grass to over one kilometre when in flight. To attach the transmitter, feathers on the back were clipped and the transmitter was glued to the remaining feather parts with cyanoacrylate, the antenna protruding behind the tail (Warnock & Warnock 1993). The transmitter would thus fall off during moult before autumn migration. During the study period 99 adult godwits were ringed (Blokland: 45, Zeevang: 54). In Blokland 22 of these godwits were equipped with a transmitter and in Zeevang 23.

Individual families were checked twice a week in 2002, 2003 and 2004 with binoculars and a 20–60× telescope. At every visit the presence or absence of families and chicks was noted and at the age of 25–35 days the number of fledglings per family was counted. Chicks were assumed to have fledged successfully if they were still alive at the fledging age of 25 days (Cramp & Simmons 1983, Schekkerman & Müskens 2000). If the exact number of fledglings could not be determined, a minimum and a maximum estimate were used. The minimum estimate was set to the number of chicks that were observed to have reached the fledging age, or to zero if a family disappeared before the chicks reached the fledging age. The maximum estimate was equal to the number of chicks that hatched in a nest, or the maximum

number possible if less chicks than that were known to be alive with certainty at some time before the fledging age. When a family disappeared from the study area immediately after hatching all chicks were assumed to have died. In about half of these cases the marked parents were resighted without chicks within 25 days after hatching, confirming that none of the young had fledged.

Weather data

Data on daily minimum temperature and duration of rainfall during the breeding season measured near Schiphol airport (c. 10 and 30 km from Blokland and Zeevang, respectively) were obtained from the Royal Dutch Meteorological Institute (KNMI). These weather data were summed over the first week after hatching (when chicks still depend on brooding by their parents for thermoregulation) and over the whole chick rearing period until fledging (25 days).

Reproductive output

Reproductive output (Y, number of fledglings produced per breeding pair) was calculated using the following formula (Schekkerman & Müskens 2000):

$$Y = (1 + R \times (1 - N)) \times N \times E \times C,$$

in which N represents nest success (the probability that a nest hatches one or more chicks), R the probability of a replacement clutch after nest failure, E the number of eggs hatching per successful nest and C chick survival until fledging. The probability of a replacement clutch (R) was assumed to be 0.5, following Schekkerman & Müskens (2000). Nest success and chick survival of replacement clutches was assumed equal to that of first clutches.

The last part of the formula, number of eggs hatched times chick survival (E × C) can be replaced by the probability that a pair raises at least one chick to fledging (S) times the number of fledglings per successful pair (F). The formula for Y can then be rewritten to:

$$Y = (1 + R \times (1 - N)) \times N \times S \times F$$

Data analysis and statistics

Nest success was calculated from daily survival rates DSR following Mayfield (1975) as $DSR^{np} \times 100\%$, in which the nest phase np (day of laying first egg to day of hatching) was assumed to be constant over years and sites at 26 days (Cramp & Simmons 1983). Chick survival was calculated by dividing the total number of chicks fledged by the total number of eggs hatched in each successful clutch.

To select the best models describing reproductive output, we used GLMs and the RSEARCH command in Genstat (Payne *et al.* 2006) using the AIC criterion.

Explanatory variables were laying and hatching dates, and year and site effects and their interactions, if significant. We explored four response variables: 1) daily survival rate of nests DSR (binomial distribution with logit link function and binomial totals of one), 2) number of eggs hatched per successful nest (binomial distribution with logit link function and binomial totals set to four, the maximum and usual number of eggs per nest), 3) minimum and maximum number of chicks fledged (chick survival, binomial distribution with logit link function and binomial totals set to the number of chicks hatched in a nest) and 4) minimum and maximum probability of a pair being successful (at least one chick fledged, binomial distribution with logit link function and binomial totals set to one), together with the total number of chicks fledged per successful pair (Poisson distribution with logarithm link function). The variables included in the models describing the four response variables are given below.

1) DSR: Godwits usually start continuous incubation after laying the last or penultimate egg (Cramp & Simmons 1983). During the laying period, the nest is often left unattended and may therefore be more vulnerable to predation (Beintema & Müskens 1987). In addition, godwits are more eager to incubate towards the end of the nest phase. Therefore we included effects of nest age in addition to those of date in the model describing the DSR. For nest age and date, a quadratic term was also included. To test these effects, we only included nests of which the start of laying was recorded with sufficient precision (see paragraph on nests and laying dates), as well as the date of hatching or failure, excluding nests that were visited less frequently than once a week. 2) The number of eggs hatched per successful nest: this metric is sensitive to both partial clutch losses (eggs disappearing due to e.g. predation) and hatching failure, and was tested for date effects. 3) Minimum and maximum chick survival and 4) minimum and maximum probability of a pair being successful: as it was sometimes difficult to determine how many chicks of a family fledged, but easier to determine whether or not any chicks fledged, we used the probability of a pair being successful, i.e. fledging at least one chick, together with the total number of chicks fledged per successful pair as an alternative measure of fledging success. We included hatching date and weather variables (cumulative minimum temperature and duration of rainfall during seven and 25 days after hatching) in the models describing minimum and maximum chick survival and the minimum and maximum probability of a pair being successful.

In addition, the age at which the last chick of a brood had disappeared before reaching the fledging age of 25 days, i.e. had presumably died, was calculated by taking the average of the age at which any chicks of a family were last recorded present, i.e. chick(s) seen or parents alarming, and the age at which they were first recorded absent, i.e. no chicks present and parents not alarming.

We used a level of significance of $\alpha = 0.05$.

Results

Breeding pair densities

Breeding pair densities were nearly three times as high in Zeevang as in Blokland, both when territories and numbers of nests are considered. In Blokland the number of breeding pairs declined during the study period from 0.150 territories ha^{-1} in 2003 to 0.094 in 2005, with a mean of 0.129 (nest densities dropped from 0.194 nests ha^{-1} in 2002 to 0.111 in 2005, with a mean of 0.189), while in Zeevang numbers fluctuated between 0.269 territories ha^{-1} in 2005 to 0.469 in 2004, with a mean of 0.364 (nest densities were 0.592 nests ha^{-1} in 2002 and 0.715 in 2004, with a mean of 0.638).

Laying and hatching dates

Median laying dates ranged between sites and years from 14 to 25 April, median hatching dates from 11 to 28 May (Table 1). After log-transformation of the laying dates, both laying date and hatching date differed significantly between years (laying: $n = 251$, $P < 0.001$; hatching: $n = 159$, $P = 0.007$), and godwits tended to both lay and hatch earlier in Zeevang, though the difference between sites was only significant for laying date ($P = 0.041$). Godwits started laying c. one week earlier in the last two years than in the first two. Hatching dates followed the pattern of laying dates.

Nest success

Daily survival rates (DSR) of nests varied between 0.937 and 0.987, resulting in a nest success varying between 19% and 71%, respectively (Table 2).

Of the five different parameters included in the model describing DSR (year, site and their interaction, nest age and date), year (aliased with the interaction of year and site), interaction of year and site ($n = 3015$, $P = 0.006$) and a linear function of nest age proved significant ($P < 0.001$). DSR tended to increase with nest age, from 0.921 when the first egg had been laid (age: 1 day), to 0.981 just before hatching (age: 25 days).

Number of eggs hatched per successful nest

The number of eggs that hatched from successful nests did not differ between years or sites and tended to decrease with hatching date, but this effect was not significant (Table 2).

Chick survival and pair success

Chick survival and probability of a pair being successful was lowest in Zeevang in 2002 (0.03–0.16 and 0.13–0.25, respectively) and highest in Blokland in that same year (0.27–0.78 and 0.44–0.81, respectively, Table 2). Both maximum chick survival and maximum probability of a pair being successful differed between years

Table 1. Median laying and hatching dates of Black-tailed Godwits in two study sites in The Netherlands in 2002–2005. Sample sizes are given between parentheses. Only nests found within 5 days from the start of laying are included for the laying date and nests visited at least once a week for the hatching date.

Year	Median laying date			Median hatching date		
	Blokland	Zeevang	Overall	Blokland	Zeevang	Overall
2002	25 April (20)	22 April (35)	22 April (55)	21 May (17)	20 May (16)	20 May (33)
2003	24 April (20)	21 April (45)	22 April (65)	28 May (17)	16 May (35)	17 May (52)
2004	14 April (25)	14 April (51)	14 April (76)	11 May (10)	11 May (27)	11 May (37)
2005	21 April (9)	15 April (46)	16 April (55)	26 May (10)	11 May (27)	13 May (27)
Overall	22 April (74)	19 April (177)	20 April (251)	22 May (54)	15 May (105)	16 May (159)

(n = 80 families, P = 0.03 and 0.042, respectively). Maximum chick survival differed between sites, being higher in Blokland than in Zeevang (P = 0.026).

Both minimum and maximum probability of a pair being successful decreased with hatching date (n = 80 families, P = 0.002 and P < 0.001, respectively). The same goes for minimum and maximum chick survival, though the effect was not significant in the former (P > 0.05 and P = 0.018, respectively). Nests of successful pairs hatched on average about one week earlier than nests of pairs which failed to fledge young.

Of all weather variables, only the cumulative minimum temperature during the first week after hatching had a significant negative effect on minimum chick survival (P = 0.022).

Of some pairs it remained unknown whether they raised any fledglings or not. Excluding these pairs did not change the outcome of these analyses.

Minimum and maximum number of fledglings *per successful pair* did not differ between years and sites and did not depend on hatching date.

The age at disappearance of the last chick did not differ between years or sites but decreased linearly with increasing hatching date (n = 26, P = 0.023, Fig. 1).

Reproductive output and timing of breeding

Mean reproductive output in the period 2002–2004 at the two study sites was estimated at 0.23–0.59 fledglings per breeding pair (Y_{min} and Y_{max} in Table 2).

Table 2. Reproductive parameters and associated reproductive output of Black-tailed Godwit at two study sites in the years 2002–2005. Min. and max. prob. success = minimum and maximum probability of a pair being successful in raising chicks. Values given in bold were used to calculate reproductive output Y (see text).

Parameter	Blokland				Zeevang				Mean
	2002	2003	2004	2005	2002	2003	2004	2005	
Nest success **N**	0.46	0.37	**0.19**	0.45	**0.22**	**0.71**	**0.28**	0.49	**0.39**
(*n* nestdays, nests)	(463, 31)	(439.5, 35)	(388.5, 37)	(210, 17)	(501, 50)	(979, 62)	(886, 76)	(724, 48)	(4591, 356)
No. hatched per successful nest **E** (SD, *n*)	**3.412** (0.712, 17)	**3.235** (1.033, 17)	**3.500** (0.850, 10)	3.182 (0.603, 11)	**3.500** (0.857, 18)	**3.605** (0.623, 43)	**3.379** (0.820, 29)	3.532 (0.654, 47)	3.464 (0.744,192)
% hatched per successful nest (SD)	88.0 (16.0)	82.4 (26.2)	87.5 (21.2)	84.1 (16.9)	87.5 (21.4)	90.7 (15.4)	87.1 (20.7)	90.4 (15.2)	**87.2** (2.85)
Min. chick survival $\mathbf{C}_{min}$ (SD, *n*)	**0.266** (0.097, 16)	**0.046** (0.030, 11)	**0.185** (0.094, 9)	-	**0.031** (0.031, 8)	**0.093** (0.053, 17)	**0.127** (0.042, 19)	-	**0.133** (0.250, 80)
Max. chick survival $\mathbf{C}_{max}$ (SD, *n*)	**0.781** (0.102, 16)	**0.205** (0.121, 11)	**0.324** (0.135, 9)	-	**0.156** (0.124, 8)	**0.226** (0.096, 17)	**0.233** (0.086, 19)	-	**0.340** (0.044, 80)
Min. prob. success S_{min} (SD, *n*)	0.438 (0.512, 16)	0.182 (0.404, 11)	0.333 (0.5, 9)	-	0.125 (0.354, 8)	0.177 (0.393, 17)	0.368 (0.496, 19)	-	0.288 (0.456, 80)
Max prob. success S_{max} (SD, *n*)	0.813 (0.403, 16)	0.273 (0.467, 11)	0.444 (0.527, 9)	-	0.25 (0.463, 8)	0.294 (0.470, 17)	0.368 (0.496, 19)	-	0.425 (0.498, 80)
Min. fledged per successful pair F_{min} (*n*)	2.14 (7)	1 (2)	1.67 (3)	-	1 (1)	2 (3)	1.14 (7)	-	1.61 (23)
Max. fledged per successful pair F_{max} (*n*)	3.31 (13)	3 (3)	2.5 (4)	-	2 (2)	2.6 (5)	2.14 (7)	-	2.77 (34)
Min. reproductive output Y_{min}	0.53	0.07	0.17	-	0.03	0.27	0.16	-	0.23
Max. reproductive output Y_{max}	1.56	0.32	0.30	-	0.17	0.66	0.30	-	0.59

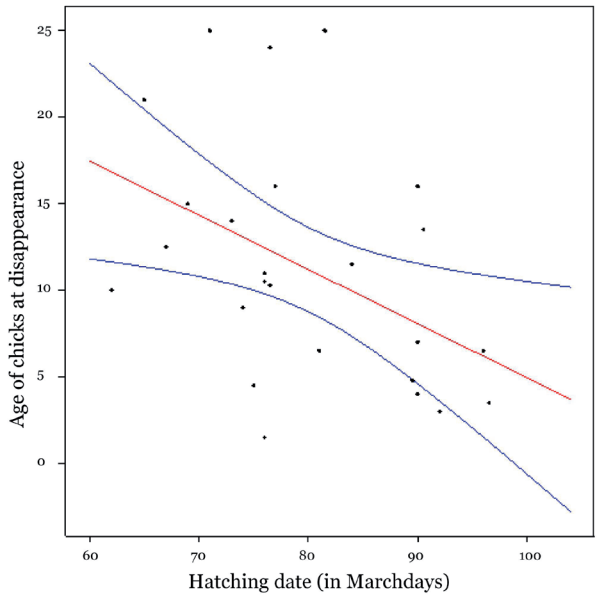

Figure 1. Estimated age at which the last chick(s) of a brood disappeared against their hatching date in days from the beginning of March (n = 26 broods, P = 0.023).

The outcomes of statistical tests on the date dependence of the probability of a pair being successful were more consistent than those on the date dependence of chick survival (see above), and estimates of pair success were probably more reliable than estimates of chick survival. Therefore we used pair success (S, calculated using the statistical model for the minimum and maximum probability of a pair being successful) multiplied by the number of fledglings per successful pair (F, Table 2) for the calculations of the date dependent reproductive output. The number of fledglings (F) per successful pair was assumed to be constant and mean minimum (1.61) and maximum (2.77) values were used. For the other variables, the year and site-specific values from Table 2 were used for the calculation of Y.

The relationships between reproductive output and laying date are shown in Fig. 2. Averaged over years and sites, the predicted number of fledglings per breeding pair decreased from c. 0.57–1.11 for clutches initiated on 28 March (first hatching date minus 26 days) to 0.22–0.59 for clutches initiated on 20 April, the median date, and 0.01–0.05 for those initiated on 26 May (last hatching date minus 26 days, final graph in Fig. 2). This means that an early nest is predicted to produce 2–2.5 times as many fledglings as a late nest, this factor being somewhat higher in Zeevang (2.5–3, median laying date 19 April) than in Blokland (1.5–2.5, median laying date 22 April, Table 1 and Fig. 2).

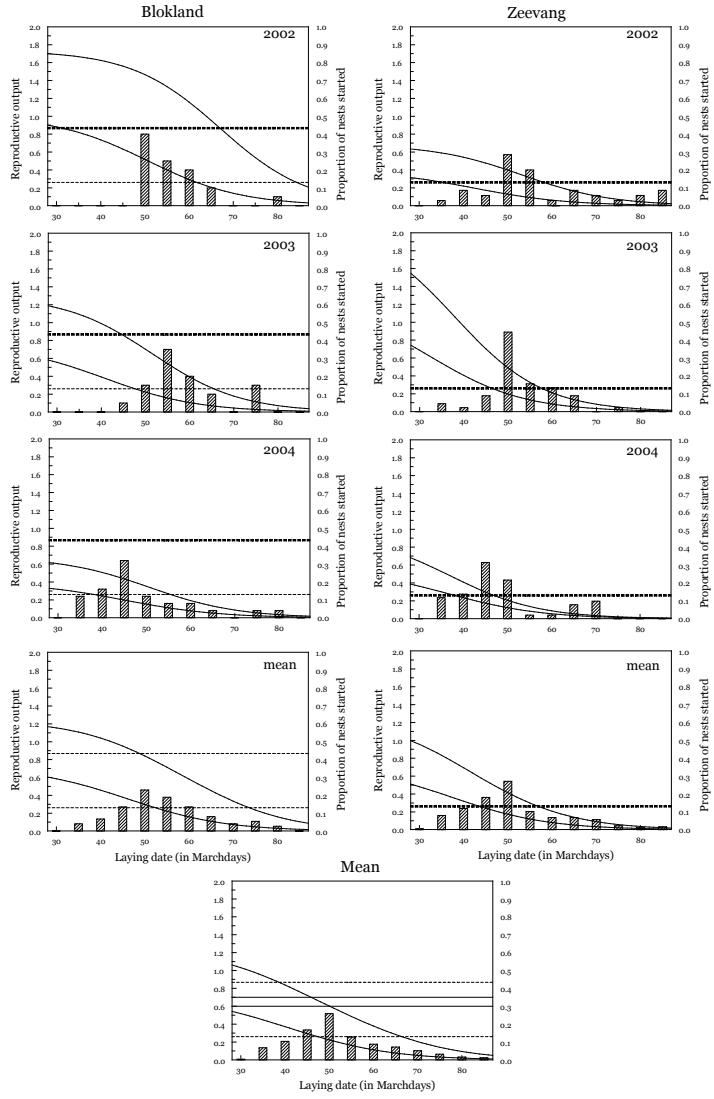

Figure 2. The predicted minimum (lower line) and maximum (upper line) reproductive output of Black-tailed Godwit (number of fledglings per breeding pair) plotted against laying date, given in days from the beginning of March, for the period 2002–2004 in two study sites. For calculation of reproductive output see text and Table 2. The dashed lines show the required reproductive output for the two populations to be stable. In the figures for Blokland the required reproductive output of Zeevang is also included, as the survival rate in Blokland may be underestimated due to a lower breeding site fidelity (see Discussion). The grey band in the lower panel indicates the required reproduction as estimated by Schekkerman & Müskens (2000, 0.6–0.7 fledglings per breeding pair). The bars represent the proportion of nests started during each five-day period.

Discussion

Nest success

The daily survival rate (DSR) of nests increased with nest age. During laying, nests are often left unattended and therefore probably run a higher risk of being detected and depredated. The DSR of nests of meadow birds has been found to be lower during laying (Beintema & Müskens 1987). In addition, at the end of the nest phase, godwits are more keen to resume incubation after disruption, which could imply a lower rate of desertion and increased incubation bouts and nest defence, decreasing predation rates. DSR does not seem to depend on the timing of laying, though the outcome may be different in areas where nests are not protected during agricultural activities and grazing and in years with severe weather in early spring. In all study years daily mean temperatures in March and April were at or above average and dropped only once below zero in 2005 at the beginning of March (based on data from 1981–2000), which may hide date effects present in other years.

Hegyi & Sasvari (1998) also did not find any effect of laying date on clutch survival in Lapwings and godwits. However, Teunissen *et al.* (2005) found a quadratic effect of date on daily survival rates of godwit and Lapwing nests, but they did not correct for effects of nest age. In their study, predation rates increased at both ends of the breeding season. As early in the season many nests are still in the laying phase, this may partly explain why early nests would have lower survival rates. However, it does not explain lower nest survival at the end of the season. If nest success declines with breeding season, reproductive output will decline even more than suggested by our results.

Chick survival and reproductive output

Except for Blokland in 2002, chick survival and reproductive output were lower than reported in most previous Dutch studies, but similar to Schekkerman *et al.* (2008a) who studied reproductive success in the same period. According to Schekkerman and Müskens (2000), each breeding pair needs to produce at least 0.6–0.7 fledglings per year to ensure a stable population, assuming an adult survival of 0.80–0.85 and first year survival after fledging of 0.6–0.7. Reproductive output reached this value only once in Blokland (in 2002) and possibly once in Zeevang (maximum, but not minimum reproductive output in 2003). Performing the same calculations with site-specific adult survival estimates of 0.93 for Zeevang and 0.81 for Blokland (Roodbergen *et al.* 2008), the reproductive output should be around 0.26 fledglings per year for the first and 0.87 for the second site. Only half of the maximum estimates (in 2002 in Blokland and in 2003 and 2004 in Zeevang) and one out of six of the minimum estimates reached these values (Zeevang 2003, Table 2). However, if apparent adult survival in Blokland is underestimated due to lower breeding site fidelity at this site (as suggested by Roodbergen *et al.* 2008) and should in reality

equal adult survival at Zeevang, reproductive output should have been sufficient at this site in 2002 (both minimum and maximum estimate), and possibly in 2003 and 2004 (maximum estimate).

It is unlikely that all adult godwits attempt to breed every year, hence the mean reproductive output of the whole population will be even lower than our estimates. Schekkerman *et al.* (2008a) show that chick survival and reproductive output have declined substantially over the past 30 years.

Timing of breeding and reproductive output

Reproductive output declined rapidly during the breeding season due to declining chick survival. This decline is probably even underestimated as parameter R, the probability of a replacement clutch after nest failure, is not constant but decreases with date and/or nest age (Schekkerman & Müskens 2000, Buker & Winkelman 1987), and as the decline in chick survival was not incorporated in the estimate of productivity from replacement clutches. At the population level, the effect of timing of breeding may even be stronger, as in many bird species, early-born chicks have a higher post-fledging juvenile survival, start breeding at a younger age and/or are more successful in their first breeding attempt (Newton & Marquiss 1984, Spear & Nur 1994).

Possible causes of decrease in chick survival with hatching date

Both chick survival and probability of a pair being successful decreased with increasing hatching date. So did the age at which the last chick of a brood had disappeared, which reinforces these findings, even if this age may not be representative for all chicks of a family. A decrease in chick survival with hatching date is found in many bird species (e.g. Spear & Nur 1994, Brinkhof *et al.* 1997, Arnold *et al.* 2004, Arnold *et al.* 2006). Among meadow birds, it has been observed in Oystercatchers (Harris 1969), Lapwings (Hegyi & Sasvari 1998) and Black-tailed Godwits (Hegyi & Sasvari 1998, Schekkerman *et al.* 2005), but not in the Redshank (Ottvall 2005).

The strong decline in chick survival, and thus in reproductive output, with hatching date may have several proximate causes.

(1) Parental quality. In many bird species, good quality and/or experienced individuals start breeding earlier than conspecifics of lower quality, and have a higher reproductive output (e.g. Newton & Marquiss 1984, Perdeck & Cavé 1992, Blomqvist *et al.* 1997, Arnold *et al.* 2004). Therefore, a correlation between timing of breeding and reproductive output may reflect parental quality rather than calendar date per se. Many studies have focused on separating timing of breeding effects from the effect of parental quality with the help of experimental manipulations (Common Terns *Sterna hirundo*: Arnold *et al.* 2004, European Coots *Fulica atra* Brinkhof *et al.* 1993, 1997). In our data we did not find any correlations between different aspects of parental quality (percentage of summer plumage, weight, condition) and hatching

date nor any difference in hatching dates of nests of godwits that did and did not return the next year (unpubl. data, MR).

(2) Weather conditions. Good weather conditions can be very important, especially for chicks in their first week, as they cannot maintain their own body temperature and need to be brooded regularly by their parents. In cold and wet weather, chicks cool down more quickly and need to be brooded more often. This leaves them less time to search for food, which may cause reduced growth and finally starvation (Beintema & Visser 1989, Schekkerman & Boele in Schekkerman 2008.). In addition, food in the form of vegetation-dwelling insects may be less available and/or less accessible in such periods. Groen & Hemerik (2002) found that chick survival is lower in cold and wet springs. In our three years of data on chick survival, however, we did not find any significant correlations with rainfall and a negative correlation between minimum chick survival and cumulative minimum temperature during the first week after hatching. This may be an artefact caused by the effect of hatching date, as minimum temperatures increase with increasing date, while chick survival decreases. The lack of an effect of rainfall or low temperatures on chick survival may be due to the above average spring temperatures in these years. In 1984, 1986 and 1987, three out of four years from the study period of Groen & Hemerik (2002), mean temperatures were below average, especially early in the breeding season. However, it does not seem likely that weather effects are responsible for the decrease in chick survival with hatching date.

(3) Food availability. Arthropod densities and biomass tend to increase in April and May, peak at the end of May and beginning of June, and decrease during the second half of June, partly due to mowing (Beintema *et al.* 1991, Schekkerman & Beintema 2007, Struwe-Juhl 1995). As chicks grow, their energy requirements increase (Schekkerman & Visser 2001), and possibly only in early chicks these requirements are met during the whole chick-rearing period. Later chicks will encounter less favourable food conditions at older ages, when energy requirements are highest. Indeed Beintema *et al.* (1991) found that daily weight gain in chicks older than 3 days declined with date. Chicks with a lower condition have a lower survival probability (Schekkerman *et al.* 2005). Although this daily weight gain already started declining at the end of May and Beintema *et al.* (1991) argue that the 'reduced growth does not correspond with a decrease in insect abundance, which takes place later', a relationship between insect abundance and chick growth cannot be excluded, as the timing of peak abundance of insects varied greatly with sampling method used and was measured in only two areas, while chick survival was based on national ringing data. Moreover, while insect abundance in preferred, uncut meadows peaks in late May, the availability of such meadows is already declining strongly before that date due to mowing. Their alternative explanation was that older chicks switch to feeding on earthworms, which become less available later in the breeding season. However, this switch seems unlikely, as we have never observed chicks feeding on earthworms,

not even around fledging (pers. obs. MR).

(4) Predation pressure. In many areas predation is the main cause of death in godwit chicks, involving different species of predatory birds and mammals. According to Schekkerman *et al.* (2008b), predation has increased since the 1980s. They estimate that 70–85% of all disappearing chicks died from predation. Their data show that in godwits the probability of a chick disappearing, which usually meant it died, increased linearly with date, while the probability that a chick was predated by a bird showed a quadratic relationship with date, increasing in May and decreasing in June (Teunissen *et al.* 2005). They also found that predation, especially by birds, was highest on meadows with short grass where chicks are more visible, which may explain the predation peak at the end of May, when most meadows have been mown.

(5) Mowing. Mowing may influence chick survival directly and indirectly. As godwit families prefer meadows with tall vegetation, the chicks repeatedly run the risk of being killed during mowing activities (Kruk *et al.* 1997, Schekkerman & Müskens 2000, Schekkerman *et al.* 2005, Teunissen *et al.* 2005). Schekkerman *et al.* (2008b) estimate that at least 5–10% of all chicks fall victim to agricultural activities. Kruk *et al.* (1997) estimate that 3–36% of the chicks present in a field died during mowing. As young chicks are more vulnerable to mowing (Kruk *et al.* 1997), this activity will have a stronger impact on late hatching broods. Mowing also negatively affects food availability, as it decreases densities of vegetation dwelling arthropods (Schekkerman & Beintema 2007, see point 3 above), and increases predation rates by removing cover (see 4). Chick survival is positively correlated with the percentage of meadows with tall vegetation during the chick-rearing period (Schekkerman *et al.* 2005). In the study sites of Schekkerman *et al.* (2005) in the years 2003–2005, 20% of the grassland area had been mown or grazed by the first week of May, while by the third week of June this percentage had increased to 100%. As the area of meadows with tall vegetation decreases, godwit families become more concentrated in these meadows and mowing and predation losses are likely to increase. Our data on mowing dates in Blokland in 2003 show that mowing started on 6 May, 22 days before the median hatching date, the percentage of area that had been mown increasing gradually until 58% on 26 June (date of last measurement). Most mowing occurred that year from 25 to 31 May, just around the median hatching date. The remaining 42% of the area, which had not been mown, was mostly grazed by cattle and/or sheep.

Parallel to chick survival, reproductive output declines in many bird species during the breeding season (Newton & Marquiss 1984, Spear & Nur 1994, Arnold *et al.* 2004, Thyen & Exo 2005, Arnold *et al.* 2006). However, increased chick mortality later in the breeding season may explain – or contribute to – population declines, if the slope of the curve describing the relationship between chick survival and hatching date has become steeper over the past decades. Beintema (1995) found a slight seasonal decrease in recovery rates of godwit chicks in the period 1976–1985, but only in wet and not in dry years. However, the advance in ringing dates in meadow bird

chicks in the period 1911–1974 described by the same author (1985) may indicate that selection pressure for early breeding has indeed become stronger. Also, if chicks that hatch late now have a lower survival than in the past, less late hatching chicks will be caught and ringed, and ringing dates will advance. However, ringing dates of Dutch godwit chicks have not shown a continued advance after the 1970s (van Santen 2000). Schekkerman (2008) extended the analysis of ringing dates of chicks of the Black-tailed Godwit in The Netherlands through 2006 and showed that since 1970 there has been no further advancement in laying date, and indeed in the four most recent years of the data set there is an unmistakable delay in laying date.

Considering the strong decline in reproductive output with laying date described in this paper, the question arises why Black-tailed Godwits did not further advance their laying dates, as this might theoretically greatly improve their breeding success and, consequently, fitness. Godwits usually arrive in The Netherlands at the end of February, at least a month before they start breeding. Timing of arrival, therefore, does not seem to be a constraint. It would be interesting to know the condition of the godwits at arrival and, being income breeders (Klaassen *et al.* 2001), how fast they can acquire enough reserves for breeding at or near their breeding grounds. Besides food, another factor which may be important for breeding is grass height: as godwits prefer to breed in tall grass, grass height may be limiting early in the season. Also, laying early may be too risky due to cold weather spells, especially if the value and/or occurrence of replacement clutches has decreased.

Management

Black-tailed Godwit reproduction rates may be greatly enhanced by facilitating early breeding, taking measures to increase nest success of early breeders, and by promoting chick survival late in the breeding season. This can be achieved by avoiding intensive grazing and other agricultural activities before and during the breeding season. Moreover, chick survival can be improved by delaying mowing and securing spatial heterogeneity, so godwits find suitable breeding habitat at any time during the breeding season. Mosaic management, a newly developed agri-environment scheme, includes the latter two recommendations, but does not sufficiently improve chick survival (Schekkerman *et al.* 2008a). However, results on effectiveness of an improved version of this type of management, in which the minimum area of suitable chick habitat available at any time was increased, look promising (Teunissen *et al.* 2007).

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4 The ongoing decline of the breeding population of Black-tailed Godwits in The Netherlands is not explained by changes in adult survival

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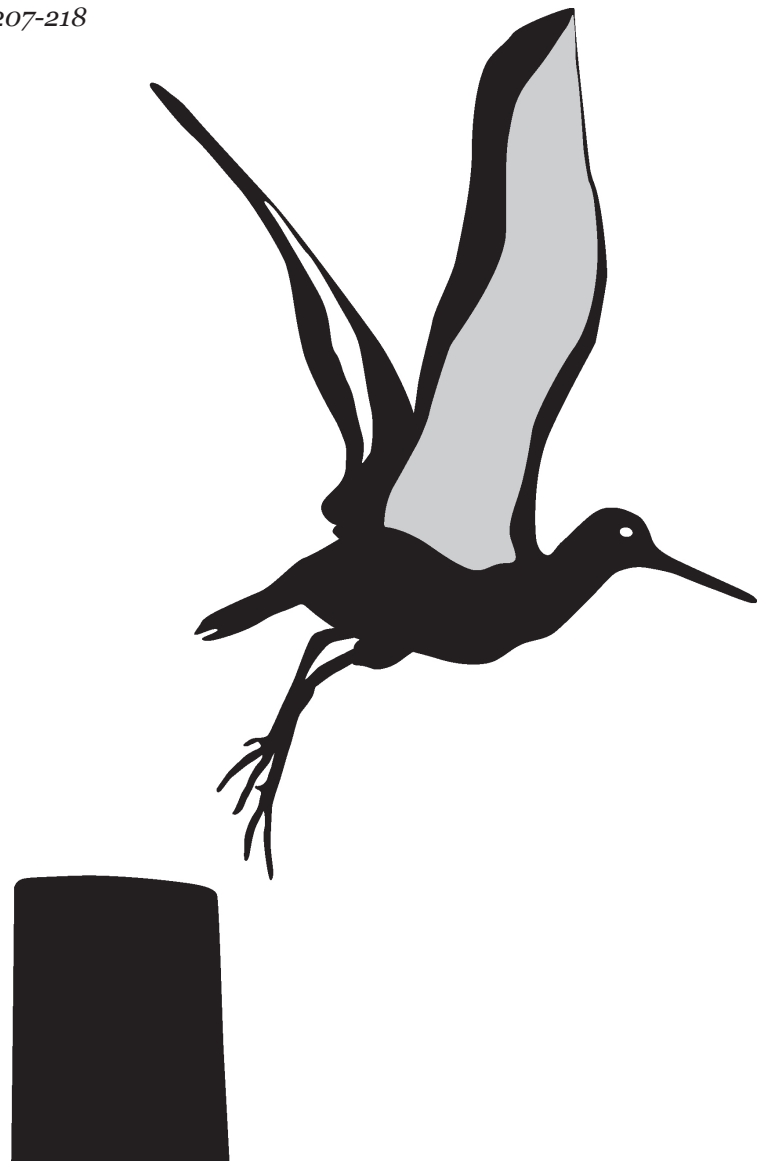

Abstract

The Black-tailed Godwit *Limosa limosa* is a characteristic breeding wader of wet grasslands in The Netherlands which has suffered a strong population decline since the 1960s. Low breeding success has been implicated as the main driver of this decline and here we examine whether changes in adult survival could also have played a role. Adult godwits were colour-ringed and resighted from 2002 through 2005 at four study sites in The Netherlands. Apparent adult survival was estimated in program MARK using Burnham's model for both live resightings and dead recoveries. In addition, nest site fidelity was estimated at two of the sites by recording the distance between nest locations in successive years. Apparent adult survival was 0.93 (SE 0.03) in one study area and 0.81 (SE 0.04) in the other three sites. Overall apparent adult survival was 0.83 (SE 0.03). These values are similar to estimates from the 1970s and 1980s. Nest site fidelity was higher in the site with highest survival (median distance between nests in successive years: 49 m vs. 252 m in the other site), suggesting that the difference in apparent survival may result from differences in emigration rates. Thus, our results suggest that current adult survival is not different from rates 30 years ago, and therefore do not point to reduced adult survival as the driver behind the current population decline of Black-tailed Godwits.

Introduction

The Black-tailed Godwit *Limosa limosa limosa* is a characteristic breeding bird in Dutch meadows, but, as in the rest of Europe, numbers have been declining rapidly (BirdLife International 2004, Teunissen *et al.* 2005a) since the 1960s (Bijlsma *et al.* 2001). Intensification of agriculture and habitat loss due to land use change are considered major causes of the decline in meadow birds (Beintema *et al.* 1995, Wilson *et al.* 2004), while more recently predation of eggs and chicks may also have played a role (Teunissen *et al.* 2005b). Around 40% of the European population of the Black-tailed Godwit breeds in The Netherlands (BirdLife International 2004), which therefore play an important role in its conservation. Agri-environment schemes, compensating farmers for restrictions posed on agricultural activities that are harmful to breeding meadow birds, have been instituted, and a widespread nest protection campaign has been employed to halt further population declines in meadow birds on agricultural lands. Despite these measures, most species continue to decline (Teunissen & Soldaat 2006).

Data on demographic parameters in recent time are now necessary for better insight into processes underlying population decline and to increase effectiveness of conservation measures. Population decline may be caused by a reduction in reproduction, survival or both (Begon *et al.* 2005). For the Black-tailed Godwit, Kruk *et al.* (1997), Schekkerman & Müskens (2000) and Schekkerman *et al.* (2008) showed that reproduction in Dutch agricultural grasslands is often low and insufficient to compensate for adult mortality. Similarly, Ratcliffe *et al.* (2005) demonstrated that flood-dependent variation in productivity is likely to explain differences in population trends at the Ouse and Nene washes in England. However, these studies have used adult survival rates based on data from the 1970s and 1980s and from the subspecies *L. l. islandica* and the validity of these predictions therefore depend on whether or not these rates have indeed changed over time or differ between subspecies. Habitat and climatic changes in wintering areas (western Africa) or at stop-over sites, such as the conversion of wetlands to rice fields (Windmeijer & Andriesse, 1993) and the decrease in rainfall (Hulme 1992, Dai *et al.* 2004), may have affected adult survival. In many European breeding birds wintering in Western Africa, adult survival is correlated with Sahel rainfall (Witstanley *et al.* 1974, Den Held 1981, Cavé 1983, Kanyamibwa *et al.* 1990, Peach *et al.* 1991, Kanyamibwa *et al.* 1993, Szep 1995, Foppen *et al.* 1999).

In The Netherlands several survival studies have been conducted. Beintema & Drost (1986) analyzed national ring recovery data from the period 1974–1980. They could only give a rough estimate for adult survival due to the low number of recoveries of godwits ringed as adult. Van Noordwijk & Thomson (2008) have recently analyzed national ring recovery data for the period 1960–2000, but they encountered problems in estimating survival rates towards the end of that period,

because the number of individuals ringed in these years was lower and the reporting rate had declined from 9% in 1960 to 1% in 2000. Groen & Hemerik (2002) estimated return rates of colour-ringed Black-tailed Godwits in Polder Schaalsmeer in 1984–1987. Between 1987 and the present study there have been no additional colour-ring studies. Reliable estimates of adult survival rates in recent time are therefore still lacking, and we cannot yet exclude reduced adult survival as a factor contributing to the population decline.

Adult mortality often cannot be distinguished from permanent emigration, especially when survival analyses are based on data from local colour-ringing studies. Therefore information on nest site fidelity is valuable to complement local studies on survival, as low nest site fidelity is likely to be associated with an increased probability of temporary or permanent movements from the study area, resulting in lower resighting probability and/or apparent survival rate.

In this paper, we report estimates of survival in four colour-ringed Black-tailed Godwit populations in The Netherlands in recent time (2002–2005) and compare these with available literature data. In two of our study sites nest site fidelity is also estimated.

Methods

Study areas

Research was carried out at four sites in The Netherlands (Fig. 1): Blokland (52°13'N, 4°49'E, province of Utrecht, c. 180 ha), Zeevang (52°31'N, 4°58'E, Noord-Holland, c. 130 ha), Schipluiden (51°59'N, 418'E, Zuid-Holland, c. 215 ha) and Delfstrahuizen (52°53'N, 5°50'E, Friesland, c. 310 ha). Current breeding densities of Black-tailed Godwits and recent population trends in these four study sites are detailed in Table 1.

The sites are a mixture of intensively and extensively used grasslands, either mown for silage or grazed by dairy cattle and sheep. In Blokland and Zeevang roughly one third of the area is under management agreements, some aiming to protect meadow birds and some to increase plant diversity. The agreements directed at protection of meadow birds usually restrict farming activities, e.g. by protecting nests during farming activities, delaying mowing dates and leaving patches unmown to facilitate cover during the fledging phase. Both sites hold high densities of breeding meadow waders, mainly Black-tailed Godwits, Lapwings *Vanellus vanellus*, Redshanks *Tringa totanus* and Oystercatchers *Haematopus ostralegus*.

Polder Blokland was reclaimed from a peat bog in the Middle Ages by diking the peat land and lowering the ground water table (Bijlmakers & de Swart 1995). To improve the soil structure and fertility, municipal waste from the cities of Amsterdam and Utrecht has been deposited here since the 16th century until 1950. Because of this deposition, the top layer of the soil has been contaminated with heavy metals and organic pollutants (Klok *et al.* 2006).

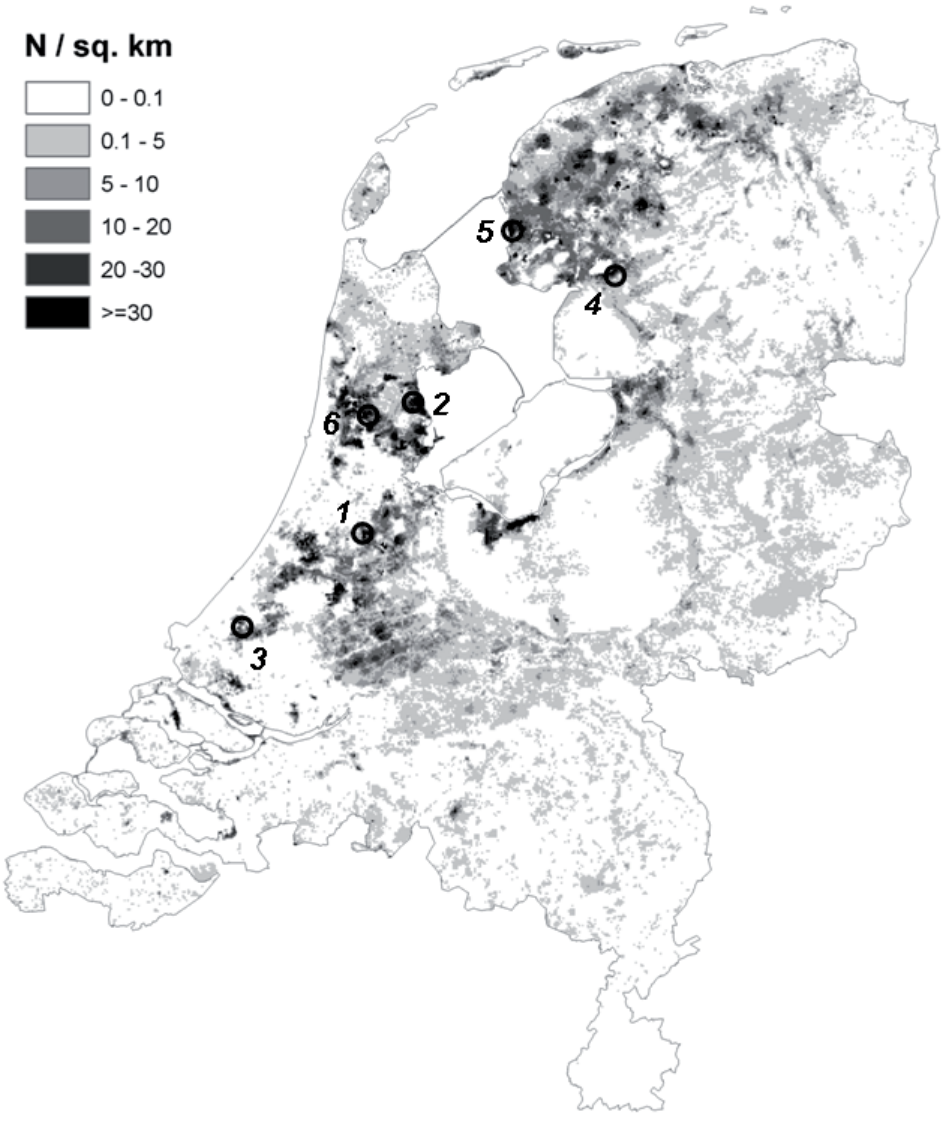

Figure 1. The distribution of the Black-tailed Godwit in The Netherlands (Teunissen et al. 2005a) and the location of six study sites. 1=Blokland, 2=Zeevang, 3=Schipluiden, 4=Delfstrahuizen, 5=Workumerwaard (Both et al. 2006), 6=Schaalsmeer (Groen & Hemerik 2002). N/sq.km = breeding pairs per km².

Table 1. Breeding densities, trends and adult survival estimates of Black-tailed Godwits at six sites in The Netherlands. Site numbers refer to the numbers in Fig. 1. Study periods are given between brackets.

Site	Current breeding density (pairs km^{-2})[1]	Trend[2]	Adult survival
1. Blokland	9–15[a]	+ (1975–1983), – (1991–2005)[abc]	0.81 (2002–2005, SD 0.04, n = 45)[l]
2. Zeevang	27–47[a]	± (1983–2006)[ad]	0.93 (2002–2005, SD 0.03, n = 54)[l]
3. Schipluiden	34[e]	+ (1973–1990), ± (1990–2005)[gh]	0.81 (2003–2005, SD 0.04, n = 17)[l]
4. Delfstrahuizen	27[e]	± (2000–2004)[f]	0.81 (2003–2005, SD 0.04, n = 16)[l]
5. Workumerwaard	32–59[i]	+ (1981–1989), ± (1989–2006)[ij]	0.95 (2004–2005, n = 65)[i]
6. Schaalsmeer	51[k]	– (1984–2001)[k]	0.81 (1984–1987, SD 0.07, n = 88)[k]

[1]the breeding density in Workumerwaard is given in nests km^{-2}
[2]+ increasing, ± stable, – decreasing

Sources: [a]Roodbergen, unpubl. data, [b]Kuijk & van Dijk 1983, [c]van den Bijtel, unpubl. data 1991, [d]Provinciale Waterstaat van Noord-Holland, unpubl. data 1985, [e]Schekkerman et al. 2008, [f]Schekkerman, unpubl. data, [g]Klemann 2002, [h]van Paassen, unpubl. data, [i]Both et al. 2006, [j]Brandsma, Hoekstra & Nauta, unpubl.data 1992, [k]Groen & Hemerik 2002, [l]this paper.

Polder Zeevang is situated near the IJsselmeer, formerly a brackish bay open to the Wadden Sea prior to closure in 1932. After the peat marshlands were drained and cultivated around 1000–1100, the dehydrated peat sank beneath sea water level and was flooded frequently by the sea, despite the many dikes and dams built in the 13th century (Heidinga 1977). The polder could only be accessed by boat and was used extensively for haymaking and livestock grazing, until large-scale redistribution of land in the 1950s, construction of roads, and further lowering of the groundwater table facilitated agricultural intensification. The area is still relatively moist in spring due to high groundwater levels.

The data from Schipluiden and Delfstrahuizen derive from an evaluation of management agreements, aiming at the conservation of Black-tailed Godwits within an economically sustainable farming practice (see Schekkerman *et al.* 2008, where detailed site descriptions can be found). At Schipluiden c. 17% of the area is under management agreements, at Delfstrahuizen this percentage is higher, 36% (H.S., unpubl. data). All areas were situated on peat, or on clay on peat soils.

Capture and ringing

Adult Black-tailed Godwits were captured on the nest using a kidney-shaped walk-in trap or a small clap net and marked with colour-rings in 2002, 2003 and 2004. Eggs were replaced by artificial eggs during capture attempts to avoid damage. Trapping was conducted at the end of incubation, when godwits are eager to incubate and the probability of abandonment of the nest is minimal (Bub 1976). At five nests, both partners were trapped and ringed, at all other nests only one incubating parent was caught. Captured godwits were measured and weighed and provided with an individual combination of darvic colour-rings and a metal ring with an individual number to facilitate individual recognition without recapture. Sex was determined from biometry and plumage characters; this may have involved a few sexing errors (Schroeder *et al.* 2008). Adult godwits were colour-ringed in Blokland (45 birds; 2002–2004), Zeevang (54 birds; 2002–2004), Schipluiden (17 birds; 2003) and Delfstrahuizen (16 birds; 2003).

Apparent adult survival

Apparent adult survival was estimated from annual return rates of marked adults. Between 2003 and 2005, the study sites and their immediate surroundings, as well as some nearby collective roosting sites (maximum distance 12 km), were searched throughout spring (from end of February to July), starting with the arrival of the first godwits, using binoculars and a telescope with magnification 20–60×. Readings were made at close range and under good conditions.

Information on live resightings and dead recoveries was collected in an encounter histories file, with sex and study site as grouping factors. Data were analyzed with the model for joint live and dead encounters of Burnham (1993) in program MARK (White & Burnham 1999). This model gives estimates for true survival (S), site fidelity (F), resighting probability of live animals (p) and reporting rate of dead animals (r), which are computed via numerical maximum likelihood techniques. Live resightings and dead recoveries were restricted to the study sites, consequently the site fidelity parameter F could not be estimated and was fixed to 1. Parameter S therefore did not represent true survival but 'local' or 'apparent' survival, which is potentially confounded with permanent emigration from the study sites.

The subset of models with different parameter constraints to be tested was based on *a priori* expectations. The reporting rate was expected to differ between Zeevang and the other sites, as in Zeevang nests were found by scanning the ground and nest search effort was high, while grassland swards were short. Furthermore, in Delfstrahuizen and in one year (2005 in Blokland and Zeevang) resighting rate was expected to be lower, due to a lower frequency of visits.

Our initial model included site and time effects (site×year) for resighting rate and survival and only site effects for reporting rate, as we did not have enough data to also include year. Next, models were simplified by testing all possible combinations

(16) of parameter constraints based on the above *a priori* expectations:
- Two different parameter sets for reporting rate *r*: *r* constant (*r*(.)), and a separate *r* for Zeevang vs. all other sites (*r*(Z)).
- Five different parameter sets for resighting rate *p*: *p* constant (*p*(.)), a separate *p* for Delfstrahuizen only (*p*(D)), a separate *p* for Zeevang and Blokland in 2005 and Delfstrahuizen combined (*p*(Z05B05D)) and a separate *p* for both Zeevang and Blokland in 2005 and for Delfstrahuizen (*p*(Z05B05,D)).
- Six different parameter sets for apparent survival *S*: *S* constant (*S*(.)) and a separate *S* for each study area (*S*(a)). Because one of our best models estimated site-specific survival (see Results), we simplified this model by including a separate *S* for each study site, by singling out each study site from the rest, which resulted in four new models (S(Z), S(B), S(D), S(S)).

We used Akaike's Information Criterion, corrected for small sample size (AICc), for model selection (Burnham & Anderson 2002). Models within 2 AICc units of the model with lowest AICc value (ΔAICc < 2) were considered to be substantially supported by the data.

The most general model (the one including all terms considered relevant, Model 14 in Table 2) was tested for overdispersion by calculating both the bootstrap Goodness of Fit ĉ and the median ĉ (White & Burnham 1999). The data were not overdispersed (bootstrap GOF ĉ = 0.912, estimated median ĉ = 0.983). The variance inflation factor ĉ was estimated with a free parameter for *F*, since GOF testing cannot be performed with fixed parameters. It gave exactly the same results for all estimated parameters (*F* = 1.0, SE < 0.01) and model deviance as the most general model with *F* fixed at 1.

Nest site fidelity

To identify the nests belonging to colour-ringed godwits, nests were observed with a telescope after disturbance, until one of the partners returned to incubate. Nest ownership was also established when a colour-ringed partner left the nest or during capture attempts. The location of the nest was determined with a GPS. From these data the distance between nests of the same individual in successive years was calculated, which was used as a measure of nest site fidelity. Throughout this paper, nest site fidelity refers to the degree of fidelity to the nest site of the previous year, expressed in distances in meters. Thus, the larger the distance between nest sites in successive years, the lower the nest site fidelity. A one-sided Mann-Whitney U test was performed to compare nest site fidelity in Blokland and Zeevang and in males and females, as we expected the nest site fidelity to be higher in the site with highest apparent survival (Zeevang, see Results) and in males (Groen 1993).

The study site in Blokland is somewhat larger and has a different shape than the site in Zeevang (180 vs. 130 ha), which might cause a bias in nest site fidelity estimates as in larger areas larger distances can be observed (van Noordwijk 1995). To correct for such a bias, we randomly and without replacement assigned returning breeders of

Table 2. Survival models for the Black-tailed Godwit and their characteristics. AICc is the Akaike's Information Criterion corrected for small sample size. S = survival probability, p = resighting probability, r = reporting rate of dead birds. Fidelity rate (F) is fixed to 1 in all models. Parameter estimates of models 1, 3 and 10 are given in Table 3.

No.	Model[1]	AICc	ΔAICc	Number of parameters	Deviance
10	S(Z)p(Z05B05D)r(Z)	313.85	0.00	6	30.40
1	S(.)p(D)r(.)	317.54	3.69	4	38.23
2	S(.)p(D)r(Z)	317.73	3.88	5	36.35
3	S(a)p(Z05B05D)r(Z)	317.81	3.96	8	30.17
4	S(.)p(Z05B05D)r(Z)	317.95	4.10	5	36.58
5	S(.)p(Z05B05D)r(.)	318.14	4.29	4	38.83
6	S(.)p(.)r(.)	318.71	4.86	3	41.45
11	S(S)p(Z05B05D)r(Z)	318.75	4.90	6	35.31
7	S(.)p(.)r(z)	318.77	4.92	4	39.46
12	S(B)p(Z05B05D)r(Z)	318.93	5.08	6	35.48
8	S(.)p(Z05B05,D)r(Z)	319.23	5.38	6	35.78
9	S(.)p(Z05B05,D)r(.)	319.23	5.38	5	37.86
13	S(D)p(Z05B05D)r(Z)	319.50	5.65	6	36.05
14	S(axt)p(axt)r(a)	343.24	29.39	28	10.61

[1]The information between brackets shows for which group a separate parameter is calculated. Groups are separated by commas. a = site, Z = Zeevang, B = Blokland, D = Delfstrahuizen, S = Schipluiden, t = time, 03 = 2003, 04 = 2004, 05 = 2005, '.' = constant. For example: S(a) p(Z05B05,D) r(Z) has a separate parameter for survival in each of the four sites, one for resighting probability in Blokland and Zeevang in 2005, one for resighting probability in Delfstrahuizen, one for resighting probability in Zeevang and Blokland in 2003 and 2004 and in Schipluiden, one for reporting rate in Zeevang, and one for reporting rate in the other three sites, and F = 1.

year x to the nests observed in the same site in year x+1. This procedure was repeated 1000 times for each year and site combination, to obtain distributions of random distances. Observed distances by year and site were compared to these distributions, and if the probability of a random value being smaller than the observed value was less than 0.05 (one-sided $\alpha = 0.05$, Dingemanse *et al.* 2003) we concluded that godwits tended to nest significantly closer to their previous nest site than expected. Finally, we calculated the differences between observed values in Blokland and those in Zeevang and between random values in both sites. The mean difference in observed distances in the two sites was said to be significant if random differences were either smaller or larger in no more than 2.5% of cases (two-sided $\alpha = 0.05$).

We estimated the number of individuals that were likely to nest outside the study

sites, and may thus not have been resighted, by drawing a circle around each nest with a radius of the site-specific median distance and estimating the area of these circles inside and outside the study site. Statistical analyses were carried out in Genstat version 9 (Payne *et al.* 2006).

Results

Apparent adult survival

In total, data on 393 bird years were collected. During the study, seven godwits were found dead, usually showing signs of predation, one godwit in each area, except in Zeevang, where four dead godwits were found (see Appendix 1).

Our initial best model (Model 1) estimated constant survival and reporting rates, and a separate resighting rate for Delfstrahuizen vs. the other three sites (Table 2). Corresponding estimates were 0.83 ± 0.03 for the overall apparent adult survival rate, 0.84 ± 0.10 for resighting rate at Delfstrahuizen, 0.97 ± 0.02 for resighting rate at the other sites and 0.13 ± 0.05 for reporting rate (Table 3). Eight other models (Models 2–9) fitted the data equally well (ΔAICc<2, as compared to Model 1). One of these models (Model 3) included site-specific survival. Estimated survival rates derived from this model suggested that survival was higher in Zeevang compared to the other three study sites (0.93 ± 0.03 in Zeevang vs. 0.82 ± 0.05 in Blokland, 0.81 ± 0.08 in Delfstrahuizen and 0.78 ± 0.08 in Schipluiden, Table 3). We then simplified the model further (following procedures outlined in the Methods) and found a new best model (Model 10, Table 2) that confirmed this notion. This model fitted the data best, with an AICc value more than 2 units smaller than all other models (ΔAICc ≥ 3.69, Table 2).

According to this model, apparent survival was 0.93 ± 0.03 in Zeevang and 0.81 ± 0.04 in the other sites (Table 3). Resighting probability was high in Schipluiden and in 2003 and 2004 in Zeevang and Blokland (0.98 ± 0.02) and somewhat lower in 2005 in Zeevang and Blokland and in Delfstrahuizen in all years (0.88 ± 0.05). Reporting rate was higher in Zeevang (0.40 ± 0.20) than in the other study sites (0.08 ± 0.05).

Nest site fidelity

The distance between nests in successive years ranged from 4 to 855 m (median 49 m) in Zeevang, and from 4 to 812 m (median 252 m) in Blokland. Nearly 60% of all nests were located within 100 m of the nest site of the previous year: 64% in Zeevang and 47% in Blokland. Nest site fidelity was higher in Zeevang than in Blokland (n_Z = 25, n_B = 15, U = 126.5, P = 0.045). When accounting for dependency in the observations by (randomly) excluding values originating from the same individuals in subsequent years, the difference was still significant (n_Z = 22, n_B = 12, U = 85.5, P = .048). After

Table 3. Parameter estimates, standard errors and 95% confidence intervals of the models 1, 3 and 10 of Table 2. Parameters are all annual rates and probabilities. See Table 2 for an explanation of models and parameters.

Parameter	Model								
	1			3			10		
	S(.)p(D)r(.)			S(a)p(Z05B05D)r(Z)			S(Z)p(Z05B05D)r(Z)		
	Estimate	SE	95%CI	Estimate	SE	95%CI	Estimate	SE	95%CI
S(.)	0.83	0.03	0.78–0.88	-	-	-	-	-	-
S(Z)	-	-	-	0.93	0.03	0.84–0.97	0.93	0.03	0.84–0.97
S(B)	-	-	-	0.82	0.05	0.72–0.89	-	-	-
S(D)	-	-	-	0.81	0.08	0.60–0.92	-	-	-
S(S)	-	-	-	0.78	0.08	0.60–0.90	-	-	-
S(BDS)	-	-	-	-	-	-	0.81	0.04	0.73–0.87
p(D)	0.84	0.10	0.54–0.96	-	-	-	-	-	-
p(ZBS)	0.97	0.02	0.90–0.99	-	-	-	-	-	-
p(Z03Z04B03B04S)	-	-	-	0.98	0.02	0.91–0.99	0.98	0.02	0.91–0.99
p(Z05B05D)	-	-	-	0.88	0.05	0.76–0.94	0.88	0.05	0.76–0.94
r(.)	0.13	0.05	0.06–0.24	-	-	-	-	-	-
r(Z)	-	-	-	0.40	0.20	0.11–0.78	0.40	0.20	0.11–0.77
r(BDS)	-	-	-	0.08	0.05	0.03–0.23	0.08	0.05	0.03–0.23

excluding pairs that remained together in both years, females tended to nest further away than males, but this difference was not significant (n_m = 10, n_f = 25, U = 88.0, P = 0.093).

Mean observed distances between nests in consecutive years were significantly smaller than mean random distances in both sites and all years (P < 0.01), except in Blokland in 2002 (P = 0.077). Mean distances observed in Zeevang were 240.3 m smaller than those observed in Blokland, while mean random distances were 56.3 m larger in Zeevang than in Blokland, but this difference was not significant (P = 0.121).

In Blokland c. 10–15% of individuals may have bred outside the study area in the next year and were thus more likely to have been missed, while in Zeevang this value was around 0–5%.

Discussion

Apparent adult survival appeared to be higher in Zeevang than in the other sites. Assuming these estimates reflect true survival and would remain constant over age and years, a godwit in Zeevang would have an adult life expectancy ($-1/(\ln S)$, Lawless 1982) of nearly 14 years, while in the other three sites life expectancy would only approach 5 years.

In this local study the fidelity parameter F cannot be estimated, and therefore it is

hard to say whether true survival, site fidelity or both are higher in Zeevang compared to the other sites. Nest site fidelity based on nests identified within the study areas tended to be higher in Zeevang than in Blokland, although the sample size was too small to draw firm conclusions. This result suggests that lower apparent survival in Blokland may be partly caused by birds moving out of the area, as illustrated by the simple analysis showing that in Blokland c. 10–15% of breeding godwits is likely to have bred outside the study area in the next year compared to 0–5% in Zeevang.

The apparent survival of 0.93 in Zeevang is in the range of the preliminary estimate of survival in the Workumerwaard in the northwest of The Netherlands (Fig. 1), where a return rate of 0.95 was found in 2004–2005 (Both *et al.* 2006). After correcting for the resighting probability, the corresponding survival rate may be even higher in Workumerwaard. In Workumerwaard nest site fidelity is probably high, as there is no suitable breeding habitat in the area surrounding the study site (Both *et al.* 2006) which might explain the high estimate for apparent survival in this population. The high apparent survival in Zeevang is also comparable to the survival of 0.87–0.94 in the *islandica* subspecies reported by Gill *et al.* (2001). *L. l. islandica* breeds almost exclusively on Iceland and winters on the coast of Western Europe (Gunnarsson *et al.* 2005a). The survival estimates for *L. l. islandica* are independent of nest site fidelity, as most resightings originate from wintering sites all over Western Europe and from spring staging sites in Iceland (Gill *et al.* 2001). Possibly, the differences in apparent survival between Blokland, Delfstrahuizen and Schipluiden on the one hand and Zeevang, Workumerwaard and Iceland on the other are primarily caused by differences in site fidelity. If so, apparent survival estimates in the first three sites are more strongly confounded with emigration rates and therefore less reliable, and possibly underestimated. More data on nest site fidelity and resightings outside the study areas are needed to see whether this is the case. Such knowledge is of high importance for effective species conservation, as in general in long-lived species a small increase in adult survival can have a disproportionately large effect on population viability as compared to a similar increase in reproduction (Stahl & Oli 2006).

Nest site fidelity is considered to be positively related to habitat quality (Groen 1993, Ganter & Cooke 1998, Badyaev & Faust 1996). Groen (1993) found that Black-tailed Godwits breeding at higher quality habitat and with successful nests are more faithful to their breeding sites. Also, breeding pair densities can be higher at better quality sites, leaving fewer vacancies and forcing individuals to remain on their former territory. Indeed, Zeevang seems a good quality site, as breeding pair densities are high in this area and, in contrast to most breeding areas in The Netherlands, the population in this study area did not decline over the last decades (Table 1). However, reproductive output in Zeevang was similar to the reproductive output in the other three areas (Roodbergen unpubl. data, Schekkerman *et al.* in press 2008) and no significant positive relation between nest success and associated

nest site fidelity could be found in the present study.

Differences in apparent survival between sites might also originate from differences in true survival, for instance due to different wintering and stopover sites, as is the case in the Icelandic godwit. In *islandica*, godwits breeding on high quality habitat also overwinter on high quality sites, and *vice versa* (Gunnarsson *et al.* 2005a,b), which is also reflected in survival (Gill *et al.* 2001). To shed more light on differences in true survival rates between Dutch breeding populations, data on wintering and stopover locations of these birds are needed.

The polluted soil at Blokland may also have negatively influenced adult survival at this site, but as apparent adult survival in Blokland was similar to that in Delfstrahuizen and Schipluiden, which are not polluted, we cannot relate the lower survival at Blokland to this factor.

The apparent adult survival in the four areas under study in the period 2002–2005 is comparable to the return rate of 0.81 in 1984–1987 estimated by Groen & Hemerik (2002, Table 1), and the rough survival estimate of 0.8 in 1974–1980 reported by Beintema & Drost (1986). These historical survival data and the data presented in this paper were probably all collected in relatively good quality habitat and do not necessarily reflect the situation in less profitable breeding areas. Yet, estimated apparent survival rates in Zeevang and Workumerwaard, which are probably more reliable than those in the other study sites, are high and resemble those found in subspecies *L. l. islandica*, whose numbers have increased substantially in recent decades (BirdLife International 2004). It is also worth noting that there is no obvious relation between the recent adult survival estimates (all within the range 0.81–0.95) and the population trends at the five sites concerned (Table 1).

Our overall survival estimate of 0.83 is even higher than the 0.77 reported by van Noordwijk & Thomson (2008), though this may also be caused by differences in methods (mostly live resightings vs. dead recoveries). Van Noordwijk & Thomson (2008) did not find strong indications for changes in either adult or juvenile survival in the period 1960 to 2000, except for a reduction in adult survival in the late 1990s. Because this occurred near the end of their study period, van Noordwijk & Thomson (2008) could not distinguish whether this was a structural decline or a short-term catastrophic event. Our data, revealing adult local survival rates in the early 21st century that are as high as values observed in 1970s and 1980s, suggest that the latter is more likely to have been the case. Therefore we conclude that our results do not support the hypothesis that the current population decline in The Netherlands is caused by a decrease in adult survival. Instead, there is evidence that the survival of godwit clutches and particularly chicks has decreased over the past decades (Schekkerman *et al.* 2008). Little is known on juvenile survival. Studies on other grassland shorebirds also do not reveal negative trends in adult survival (Lapwing, Bak & Ettrup 1982, Peach *et al.* 1994; Redshank, Thompson & Hale 1993, Insley *et al.* 1997, Ottvall 2005; Oystercatcher, Neve & van Noordwijk 1997, Atkinson *et al.*

2005), while reproduction has declined in most species (Hulscher & Verhulst 2003, Besbeas *et al.* 2002, pers. comm. H. Hötker).

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Appendix 1.

Summary of the live and dead encounters input file used for the survival analysis in MARK. Occ. = occasion of release, j = year in which godwits released at occasion i are resighted or reported respectively. For live recapture data, the number of releases (R(i)) are shown on the left side, and the number of live recaptures for each occasion is shown for each set of releases. For dead recovery data, the number of releases for the last live release (R(i)) is shown on the left side, and the number of dead recoveries for each occasion and release is shown.

Live encounters						
Study site	Occ.	R(i)	j= 2	3	4	Total
Zeevang	1	19	15	1	0	16
	2	31		29	0	29
	3	49			41	41
Blokland	1	23	20	0	0	20
	2	30		21	1	22
	3	33			25	25
Delfstrahuizen	1	0	0	0	0	0
	2	16		9	2	11
	3	9			8	8
Schipluiden	1	0	0	0	0	0
	2	17		13	0	13
	3	13			10	10

Dead recoveries							
Study site	Occ.	R(i)	j= 1	2	3	4	Total
Zeevang	1	3	2	0	0	0	2
	2	2		1	0	0	1
	3	8			0	0	0
	4	41				1	1
Blokland	1	3	0	0	0	0	0
	2	8		1	0	0	1
	3	8			0	0	0
	4	26				0	0
Delfstrahuizen	1	0	0	0	0	0	0
	2	5		1	0	0	1
	3	1			0	0	0
	4	10				0	0
Schipluiden	1	0	0	0	0	0	0
	2	4		1	0	0	1
	3	3			0	0	0
	4	10				0	0

5 Diagnosing declining grassland wader populations using simple matrix models

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Maja Roodbergen
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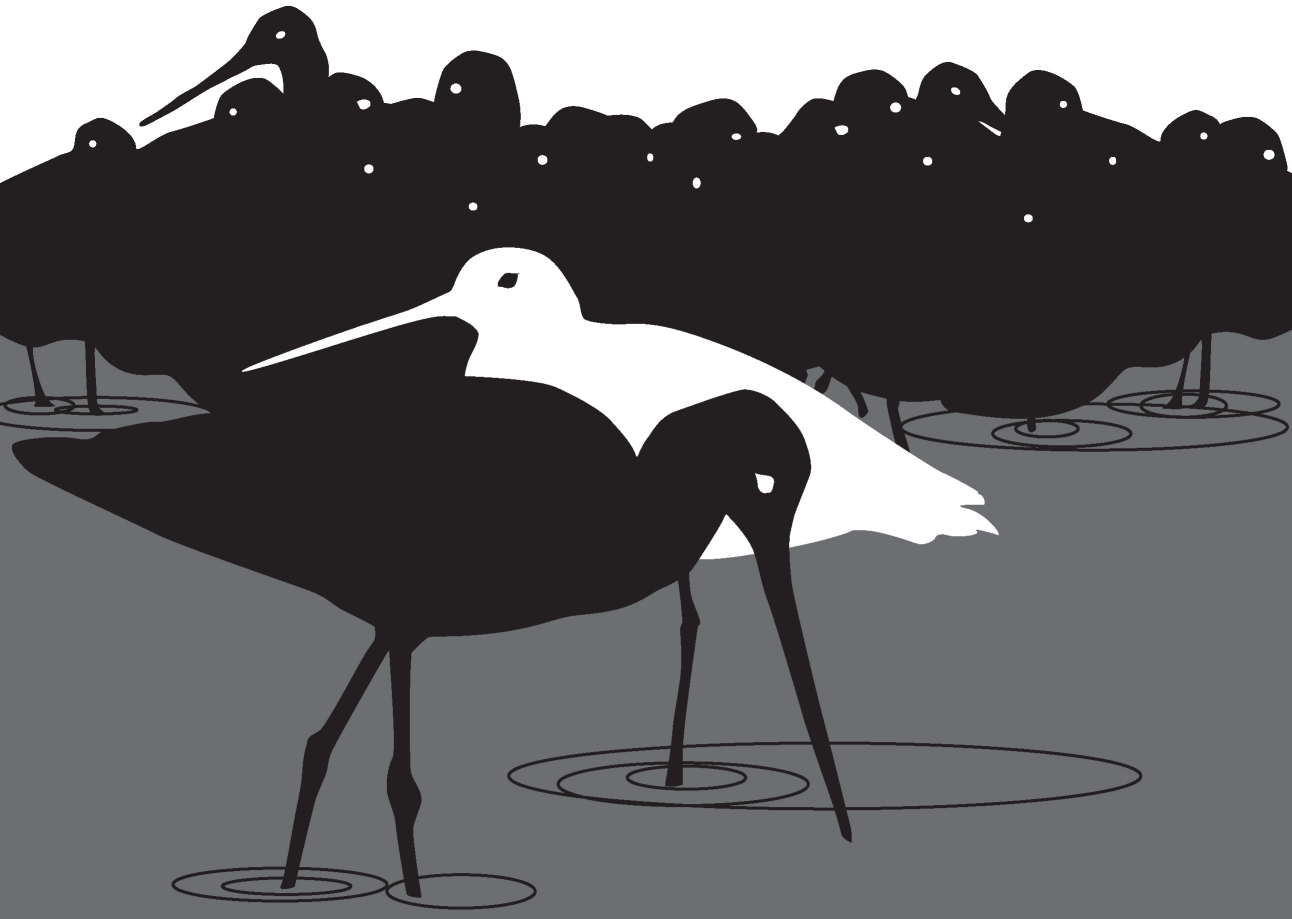
Animal Biology 59 (2009): 127-144



Abstract

Many populations of wader species have shown a strong decline in number in Western-Europe in recent years. The use of simple population models such as matrix models can contribute to conserve these populations by identifying the most profitable management measures. Parameterization of such models is often hampered by the availability of demographic data (survival and reproduction). In particular, data on survival in the pre-adult (immature) stage of wader species that remain in wintering areas outside Europe are notoriously difficult to obtain, and are therefore virtually absent in the literature. To diagnose population decline in the wader species; Black-tailed Godwit, Curlew, Lapwing, Oystercatcher, and Redshank, we extended an existing modelling framework in which incomplete demographic data can be analysed, developed for species with a pre-adult stage of one year. The framework is based on a Leslie matrix model with three parameters: yearly reproduction (number of fledglings per pair), yearly pre-adult (immature) and yearly adult (mature) survival. The yearly population growth rate of these populations and the relative sensitivity of this rate to changes in survival and reproduction parameters (the elasticity) were calculated numerically and, if possible, analytically. The results showed a decrease in dependence on reproduction and an increase in pre-adult survival of the population growth rate with an increase in the duration of the pre-adult stage. In general, adult survival had the highest elasticity, but elasticity of pre-adult survival increased with time to first reproduction, a result not reported earlier. Model results showed that adult survival and reproduction estimates reported for populations of Redshank and Curlew were too low to maintain viable populations. Based on the elasticity patterns and the scope for increase in actual demographic parameters we inferred that conservation of the Redshank and both Curlew populations should focus on reproduction. For one Oystercatcher and the Black-tailed Godwit populations we suggested a focus on both reproduction and pre-adult survival. For the second Oystercatcher population pre-adult survival seemed the most promising target for conservation. And for the Lapwing populations all demographic parameters should be considered.

Introduction

In the second half of the 20th century, widespread changes in European land use resulted in drastic declines in many farmland bird populations (Gregory *et al.* 2005; Donald *et al.* 2006). Agricultural intensification has been identified as the main driver behind this biodiversity loss (e.g. Tucker and Heath, 1994; Gregory *et al.* 2005). The Common Agricultural Policy of the European Union (EU) played a large role in land use change, and is expected to have similar dramatic effects in former eastern European countries that are now joining the EU (Van Strien *et al.* 2001).

An important group of farmland bird species characteristic of European agricultural meadows are grassland waders, including species such as Black-tailed Godwit (*Limosa limosa*), Lapwing (*Vanellus vanellus*), Redshank (*Tringa totanus*), Oystercatcher (*Haematopus ostralegus*), and Curlew (*Numenius arquata*). These wader species are characterized by a long life-span and a low rate of reproduction. The average age at which these species start breeding varies from one (Redshank) to about five years (Oystercatcher) (Cramp and Simmons, 1983). Per year they can raise only one brood with a maximum of four chicks to fledging (Cramp and Simmons, 1983).

In Western-Europe in the last decade of the 20th century, populations of the Black-tailed Godwit and Lapwing showed a large decline in number (>30%), while numbers of Redshank, Oystercatcher and Curlew showed a more moderate decline (10-29%). All species except the Oystercatcher are classified as declining or vulnerable according to the EU25 threat status (BirdLife International, 2004).

In the Netherlands, agricultural meadows have become an important, if not vital, breeding habitat for wader species (Beintema, 1986). Their dependence on man-made habitat makes this group vulnerable to agricultural intensification. Many different conservation measures have been taken in the form of agri-environment schemes, but their effectiveness has been much debated (e.g. Kleijn *et al.* 2001; Wilson *et al.* 2007). For effective conservation, a good understanding of the population dynamics of a species is essential (Caswell, 2001). However, good data on demographic parameters (survival and reproduction) of species are often missing. All meadow birds are (semi-)precocial, indicating that they leave the nest when hatched. This complicates reliable estimation of the number of fledglings per pair. In addition, sub-adult survival (from post fledging age to age of first reproduction) is hard to estimate as immature individuals show lower site fidelity than adults and may remain in the wintering areas during their first year(s) of life. To overcome this data-scarcity problem, Hemerik and Klok (2006) developed a population model in which a single missing demographic parameter from the full set can easily be estimated visually if the population trend is known. Their model is applicable for species with a pre-adult stage of one year.

The aim of this paper was to estimate the population viability of five wader species: Redshank, Black-tailed Godwit, Curlew, Lapwing and Oystercatcher, using a population model in which incomplete demographic data can be analysed. To analyse wader species with a pre-adult stage of more than one year (Black-tailed Godwit, Curlew, Lapwing and Oystercatcher), we first extend the population model developed by Hemerik and Klok (2006). The model gives information on the yearly population growth rate and its elasticity (the proportional change in the yearly population growth rate given an infinitesimal proportional change in one of the demographic parameters). Secondly, data from literature on population status and demographic parameters of the five wader species are assembled and projected in the resulting plots of the applicable model, in order to analyse the yearly population growth rate and to infer information on the missing demographic parameter. The available data on wader species generally lack information on pre-adult survival. Therefore, we relate adult survival to both pre-adult survival (as in Hemerik and Klok, 2006) and to reproductive output.

Material and methods

Model development

We extended the general stage structured model of Hemerik and Klok (2006) for species that start breeding at an age older than one year, such as Black-tailed Godwit (3rd calendar year), Curlew (probable 3rd calendar year), Lapwing (3rd calendar year), Oystercatcher (5th calendar year) (Cramp and Simmons, 1983). In our model only females are explicitly taken into account, and we assumed that (a) the sex ratio is 1:1, (b) the population growth rate is independent of density, (c) the survival of females is equal to that of males, and (d) breeding takes place in a short period in spring (in technical terms a pulse, Caswell, 2001 p25-27). We sampled (censused) the model yearly just after juveniles have fledged (post-breeding). Figure 1 shows a simplified life cycle graph used for the model.

Yearly population growth rate

The life cycle graph in Fig. 1 can conveniently be described in mathematical form. Here, we exemplify our model with a Leslie matrix for a life cycle with a pre-adult stage of two years. A general description for life cycles with a pre-adult stage of one to T years is given in the appendix.

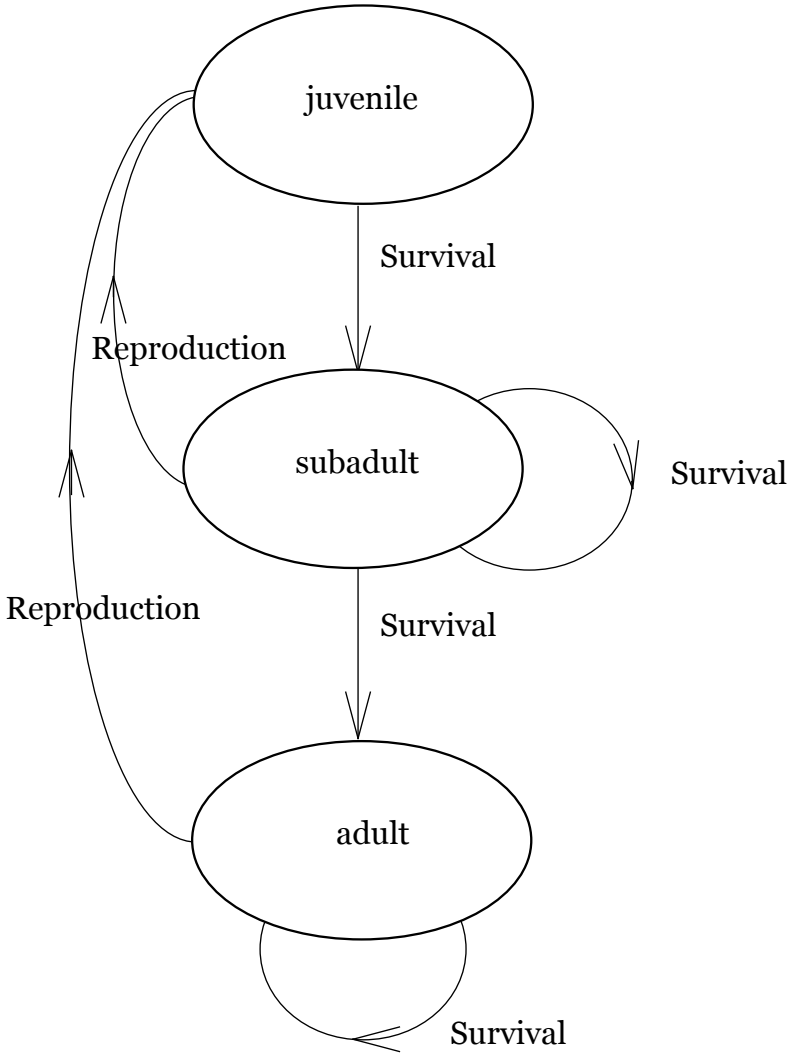


Figure 1. Simplified life cycle graph as used for the models with a two or four year pre-adult life stage (T=2 or 4). With a pre-adult life stage of two years individuals spend one year in the juvenile and one in the sub-adult stage, whereas with a pre-adult life stage of four years, one year is spend in the juvenile and three in the sub-adult stage.

The change in number of individuals in the three stage classes over the years can be assessed with equation 1 (this is an extension of eqn. 4 in Hemerik and Klok, 2006),

$$\begin{pmatrix} j_{t+1} \\ s_{t+1} \\ g_{t+1} \end{pmatrix} = Z_3 \begin{pmatrix} j_t \\ s_t \\ g_t \end{pmatrix} \qquad \text{with} \qquad Z_3 = \begin{pmatrix} 0 & q\frac{m}{2} & a\frac{m}{2} \\ q & 0 & 0 \\ 0 & q & a \end{pmatrix} \tag{1}$$

Here q equals yearly survival of individuals from the age of fledging until the age of adulthood (T, here 2), a yearly survival of adult birds and the subscript 3 indicates a Leslie matrix with 3 age classes. The number of fledged young per pair per year is represented by m. When the census of the model is just after juveniles fledged (post-breeding), j_t represents the number of juveniles (aged 0^+; birds in their first year), s_t the number of sub-adult birds (aged 1^+) and g_t the number of adult birds in year t (aged 2^+).

Given an initial population in the different age classes, the change over the years can be assessed by iterating matrix Z_3. Under non-changing environmental conditions the population eventually grows at a yearly factor that equals the dominant (i.e. absolute largest) eigenvalue of matrix Z_3. This dominant eigenvalue (λ) is directly related to the intrinsic population growth rate $r = \ln \lambda$ (Caswell, 2001). We calculated the dominant eigenvalue for values of q and a (from 0.001 to one, step 0.001) and relevant values of m for the Leslie matrix with a pre-adult stage of two years (Eq. 1) and show the line where the population growth rate equals zero (dominant eigenvalue $\lambda = 1$), which separates parameter combinations where the population goes extinct ($r<0$, $\lambda<1$) from the combinations where the population is viable ($r>0$, $\lambda>1$). Furthermore, we show this line as a function of a and m for Leslie matrices with a pre-adult stage of one, two and four years (see appendix for the general matrix with a pre-adult stage of T years).

Elasticity analysis

Caswell (2001) gives formulas for defining the elasticity of matrix entries (z_{ij}) and underlying parameters of a matrix Z_3, by calculating explicitly the right and left eigenvectors for the dominant eigenvalue of the matrix. These eigenvectors have biological meaning; the right eigenvector (a column vector x for which $Z_3x = \lambda x$) represents the stable age distribution, i.e. the composition of the population in age classes that the population can attain in the long run. The left eigenvector (a row vector y for which $yZ_3 = \lambda y$) gives the reproductive values, i.e. the expected relative reproductive output of the different age classes. We derived the elasticities of the lower level parameters a, q and m of Z_3 using implicit differentiation of the characteristic equation $\det(Z_3 - \lambda I) = 0$. The characteristic equation $f_3(\lambda) = 0$ of this

matrix is given in Eq. (2). For convenience, the derivative with respect to λ is denoted $f_3'(\lambda)$

$$f_3(\lambda) = \lambda^3 - a\lambda^2 - \frac{mq^2}{2}\lambda = 0 \quad (2)$$

The elasticity of a general lower level parameter h (here m, a, q) of matrix Z_3 is defined as:

$$e_3(h) = \frac{h\partial\lambda}{\lambda\partial h} \quad (3)$$

From implicit differentiation of Eq. (2) we can derive $\frac{\partial\lambda}{\partial h}$. Multiplying the result with $\frac{h}{\lambda}$ yields the elasticities:

$$e_3(a) = \frac{a\lambda}{f_3'(\lambda)}, e_3(q) = \frac{mq^2}{f_3'(\lambda)} \text{ respectively } e_3(m) = \frac{mq^2}{2f_3'(\lambda)} \quad (4)$$

The derivation of the elasticity of the underlying parameters of a Leslie matrix with a pre-adult stage of T years is given in the appendix.

The elasticity of an underlying parameter has biological meaning: it quantifies the effect of relative change in a parameter value in terms of a relative change in the population growth rate.

Literature-derived demographic data for five wader species

We selected population studies on the five species of meadow birds from published literature, based on the completeness of the presented set of demographic parameters. We selected only those studies that reported data on at least two of the following parameters: pre-adult survival, adult survival, and/or reproduction, complemented with data on population trends.

Results

Yearly population growth rate

The largest eigenvalue (λ) for the 3x3 Leslie matrix Eq. 1 was analytically derived as.

$$\lambda = \frac{a}{2} + \frac{\sqrt{a^2 + 2q^2m}}{2}$$

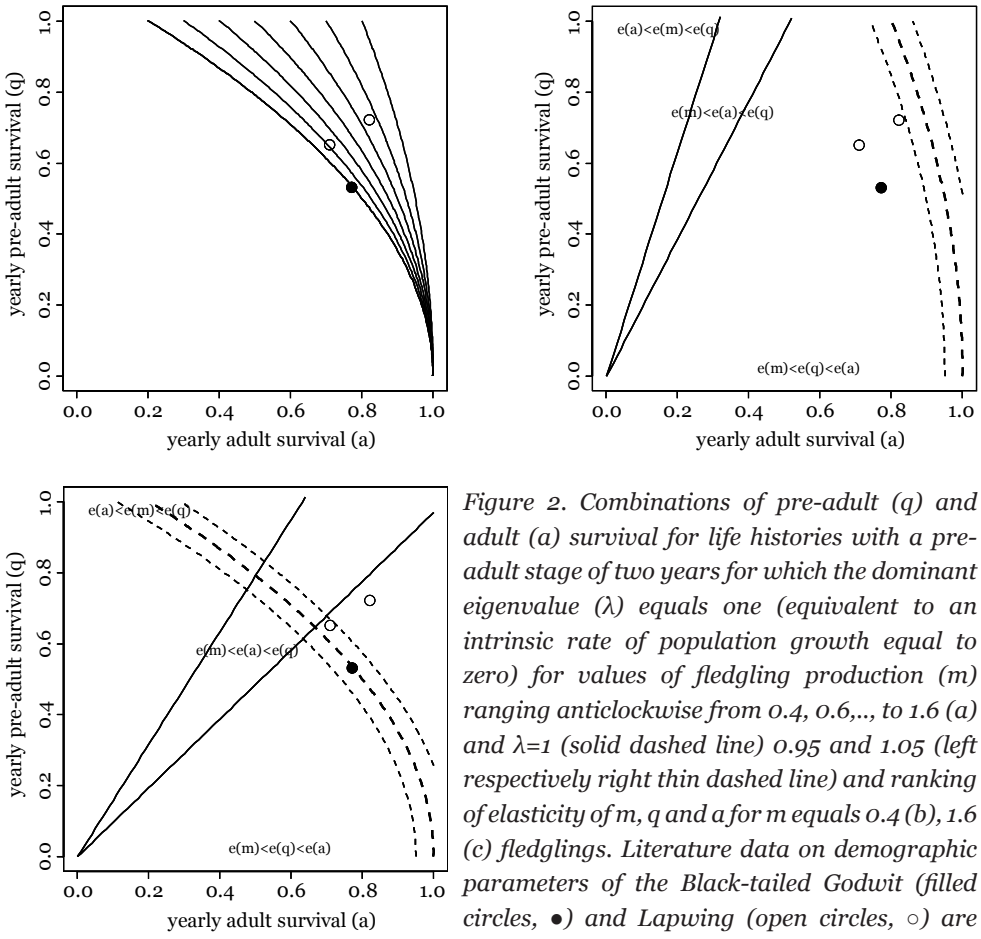


Figure 2. Combinations of pre-adult (q) and adult (a) survival for life histories with a pre-adult stage of two years for which the dominant eigenvalue (λ) equals one (equivalent to an intrinsic rate of population growth equal to zero) for values of fledgling production (m) ranging anticlockwise from 0.4, 0.6,.., to 1.6 (a) and λ=1 (solid dashed line) 0.95 and 1.05 (left respectively right thin dashed line) and ranking of elasticity of m, q and a for m equals 0.4 (b), 1.6 (c) fledglings. Literature data on demographic parameters of the Black-tailed Godwit (filled circles, ●) and Lapwing (open circles, ○) are included (see Table 1).

Lines in the adult (*a*), and pre-adult (*q*) survival plane, where the largest eigenvalue equals one (implying an intrinsic rate of population growth of zero) for the 3x3 Leslie matrix, are drawn in Figure 2a for a number of fledglings produced per pair (*m*) equal to 0.4, 0.6,..,1.6. The parameter space to the right and above the lines indicates combinations of *a* and *q* where the population is viable (λ>1). With a higher value of *m*, the part of the parameter space where a population is viable increased (Fig. 2a). From the perspective of conservation of a species, not only λ =1 but also the parameter space around it is of interest. In Figure 2b and 2c we therefore indicated the combinations of *q* and *a* for which λ∈(0.95, 1.05) (between thin dotted lines). This illustrates the uncertainty in λ from the demographic parameters for *m* values of 0.4 (Fig. 2b) and 1.6 (Fig. 2c). The elasticities of the three lower level parameters *a*,

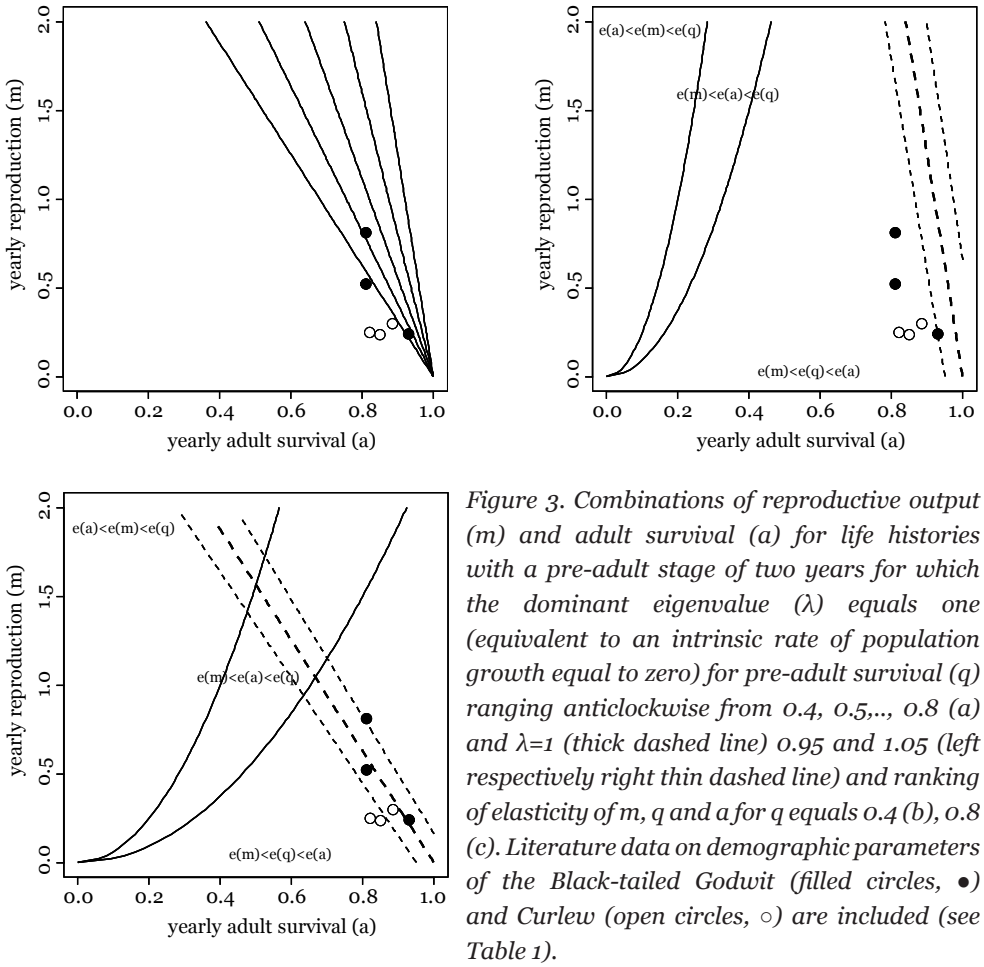


Figure 3. Combinations of reproductive output (m) and adult survival (a) for life histories with a pre-adult stage of two years for which the dominant eigenvalue (λ) equals one (equivalent to an intrinsic rate of population growth equal to zero) for pre-adult survival (q) ranging anticlockwise from 0.4, 0.5,.., 0.8 (a) and λ=1 (thick dashed line) 0.95 and 1.05 (left respectively right thin dashed line) and ranking of elasticity of m, q and a for q equals 0.4 (b), 0.8 (c). Literature data on demographic parameters of the Black-tailed Godwit (filled circles, ●) and Curlew (open circles, ○) are included (see Table 1).

q and m are proportional with ratios $\frac{2a\lambda}{mq^2}$:2:1. This is illustrated in Figs. 2bc, which shows that, for the larger value of m (1.6; Fig. 2c), the area where pre-adult survival (q) has the largest elasticity, is small compared to the same area in Fig 2b (m =0.4).

Figure 3 is similar to Fig. 2 but now the lines with λ=1 (Fig. 3a) are depicted in the adult survival (a) and number of fledglings per pair (m) plane, for values of sub-adult survival (q) varying from 0.4, 0.5,.., 0.8. As in Fig. 2a, the population is viable ∈(λ>1) above and to the right of the lines. Figs. 3bc show the line λ=1 (thick dashed) and the space around this line where λ(0.95, 1.05) (between thin dotted lines) for q

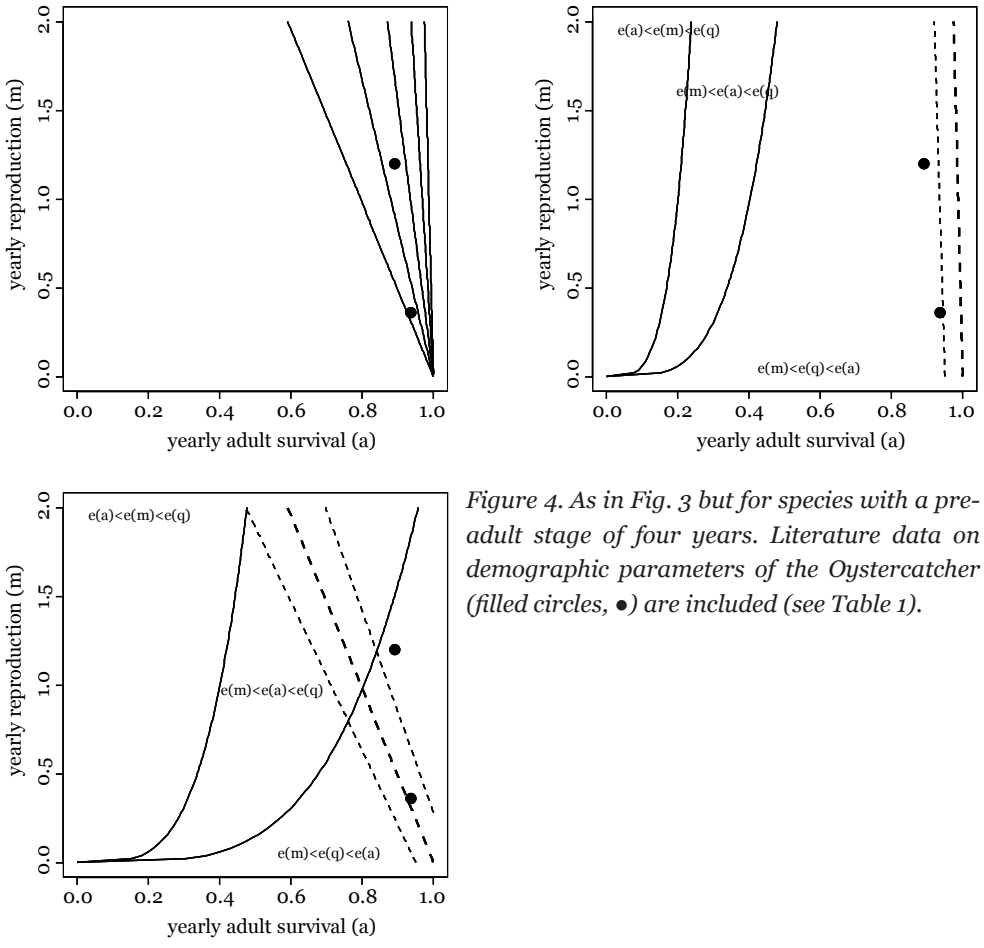


Figure 4. As in Fig. 3 but for species with a pre-adult stage of four years. Literature data on demographic parameters of the Oystercatcher (filled circles, ●) are included (see Table 1).

values equal to 0.4 (Fig. 3b) and 0.8 (Fig. 3c), moreover, the ranking of elasticities is depicted. A larger value of *q* resulted in a larger area of the parameter space in which the population is viable. In addition, the area where *q* has the highest elasticity increased, whereas the area where the elasticity of *a* is higher decreased (compare Fig. 3c with 3b).

The derivation of the characteristic equation for an *n* x *n* Leslie matrix with the same general structure is given in the appendix. For Leslie matrices larger than 4x4 the analytical derivation of the largest eigenvalue resulted in a complicated form, and therefore can easier be solved numerically. The derivation of the elasticities of the underlying parameters is also given in the appendix. Elasticities of the parameters

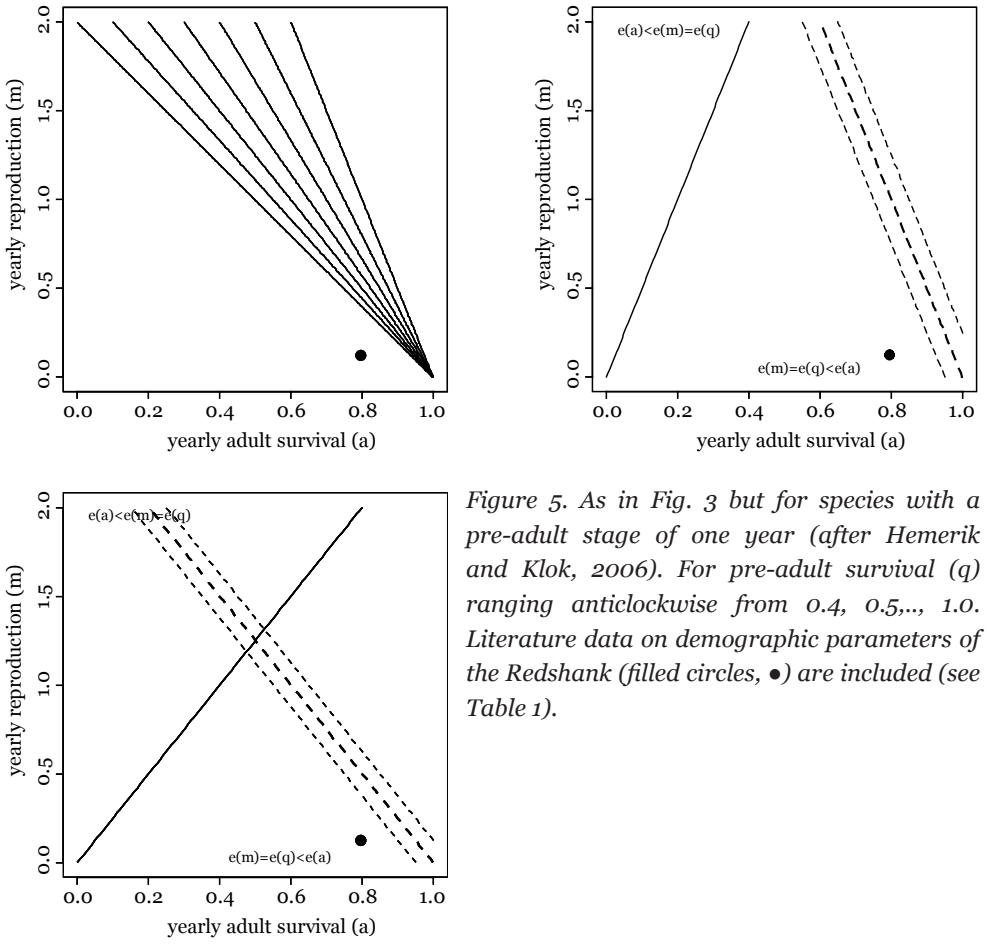


Figure 5. As in Fig. 3 but for species with a pre-adult stage of one year (after Hemerik and Klok, 2006). For pre-adult survival (q) ranging anticlockwise from 0.4, 0.5,.., 1.0. Literature data on demographic parameters of the Redshank (filled circles, ●) are included (see Table 1).

a, *q* and *m* are proportional with ratios $\frac{2a\lambda^{n-1}}{mq^{n+1}}$:n+1:1, with *n* the duration of the pre-adult stage. This equation indicates that the elasticity of *m* is always smaller than the elasticity of *q* and *a* (with the exception of life-histories with a pre-adult stage of one year, where e(*m*)=e(*q*)).

To illustrate the model for the Oystercatcher and Redshank we also depicted the yearly population growth rate and elasticity results of a 5x5 (Fig. 4) and 2x2 Leslie matrix (Fig. 5) in the *a*, *m* plane similar to Figure 3.

As can be inferred from Fig. 5a, 3a and 4a (respectively pre-adult stage of one,

two and four years), an increase in the duration of the pre-adult stage results in more steep lines λ=1, showing lower dependence on *m* values. This implies that the pre-adult survival (*q*) must increase for a population to remain viable for a certain combination of *a* and *m*. This is also apparent from the "equal" elasticity lines in Fig. 3b,c to 5b,c: the area, where *q* has the highest elasticity, increased with the duration of the pre-adult stage, while the area, where *a* has the highest elasticity, decreased.

Inference on missing demographic parameter

Table 1 summarizes the available data on the population status, survival and reproduction in the five wader species in western Europe. Data on pre-adult survival are missing for three species, and data on reproduction are absent for the Lapwing. For the two Oystercatcher populations and one Black-tailed Godwit population, full data on demographic parameters were reported (Harris, 1967; Schnakenwinkel, 1970; Groen and Hemerik, 2002). Most survival estimates are based on live resightings based on return rate only (Table 1).

The demographic data (Table 1) of the five wader species are plotted in Figs. 2 to 5 and the inference from these graphs on the missing demographic parameter is given in Table 1. For example it can easily be inferred graphically from the figures that populations cannot be viable for two reported datasets on Curlew (Fig. 3a) and Redshank (Fig. 5a). For all data sets adult survival has the highest elasticity suggesting that this demographic parameter is an important target for management.

Discussion

Most data on survival (Table 1) are based on live resightings, and estimates are not corrected for resighting probability. In resighting studies, dispersal from the study site cannot be separated from mortality, and therefore survival in these studies tends to be underestimated (Lebreton *et al.* 1992). Not correcting for resighting probability will further depress survival estimates, which indicates that survival values of the populations in Table 1 are probably higher than reported.

For the two Lapwing populations, the model suggests a number of fledglings per pair (*m*) of 0.69 and 1.36 respectively, which is higher than the average of wader productivity estimates reported in the literature, which falls below 0.5 (Roodbergen *et al.* in prep). With a number of fledglings per pair (*m*) <0.5, the population can only be viable (λ>1) if both pre-adult and adult survival reaches values of 0.8 or more (read from Fig. 2a), whereas the reported estimates for adult survival in waders range from 0.6-0.83 (Roodbergen *et al.* in prep). Based on these data we suggest future management of these declining populations to focus on adult and pre-adult survival (inferred from the elasticity pattern Fig. 2c) and reproduction.

Our model result on pre-adult survival (*q*) for the Black-tailed Godwit population

*Table 1. Estimates of demographic parameters reported in the literature for Redshank (*Tringa totanus*), Lapwing (*Vanellus vanellus*), Black-tailed Godwit (*Limosa limosa*), Curlew (*Numenius arquata*) and Oystercatcher (*Haematopus ostralegus*). Not all authors give the standard deviations and therefore just the means are given. Population trend is coded as −/0/+ for declining, stable and increasing populations respectively.*

Species	Country	Period	Fledgling production (m)	1st year survival	Adult survival (a)	Method+	Population trend	Conclusion based on calculations
Redshank[1]	Sweden	1997-2003	0.125	nr	0.797	L	0	$\lambda<1$ for all possible values of q
Lapwing[2]	Great-Britain	1963-1998	nr	0.63	0.82	D	-	$\lambda>1$ if $m>0.69$ (based on $q = \sqrt{(0.63\ 0.82)}$
Lapwing[3]	Great-Britain	1930-1988	nr	0.6	0.71	D(Haldane)	-	$\lambda>1$ if $m>1.36$ (based on $q = \sqrt{(0.6\ 0.71)}$
Black-tailed Godwit[4]	Netherlands	1984-1987	0.81	0.19	0.81	L(r)	-	$\lambda>1$ if $q>0.68$
Black-tailed Godwit[5, 6]	Netherlands	2002-2005	0.24	nr	0.93	L	0	$\lambda>1$ if $q>0.77$
Black-tailed Godwit[5,6]	Netherlands	2002-2005	0.52	nr	0.81	L	-	$\lambda>1$ if $q>0.86$
Black-tailed Godwit[7]	Netherlands	1960-2000	nr	0.36	0.77	D	-	$\lambda>1$ if $m>1.66$ (based on $q = \sqrt{(0.36\ 0.77)}$
Curlew[8]	N-Ireland	1993-1995	0.235	nr	0.85	L(r)	-	$\lambda<1$ for all possible values of q
Curlew[9]	Sweden	1985-1992	0.25	nr	0.82	L(r)	+	$\lambda<1$ for all possible values of q
Curlew[10]	Germany	1973-1980	0.3	nr	0.885	L(r)	-	$\lambda>1$ if $q>0.88$
Oystercatcher[11]	Germany	1949-1962	0.36	0.5*	0.937	L(r)	+/0	$\lambda>1$ if $q>0.77$
Oystercatcher[12]	Wales	1963-1965	1.2	0.6	0.89	L(r)	0	$\lambda>1$ if $q>0.65$

nr = not reported, q = pre-adult survival,+:L = live resightings, (r) = return rate only, not corrected for resighting probability, D = dead recoveries, (Haldane) = Haldane's method, not corrected for reporting probability (see Roodbergen et al. in prep.),: 1st & 2nd year.*

[1]: Ottvall, 2005, [2]: Besbeas et al. 2002, [3]: Peach et al. 1994, [4]: Groen and Hemerik, 2002, [5]: Roodbergen et al. in press, [6]: Roodbergen and Klok, in press, [7]: van Noordwijk and Thomson, 2008, [8]: Grant et al. 1999, [9]: Berg, 1991, [10]: Kipp, 1982, [11]: Schnakenwinkel, 1970, [12]: Harris, 1967.

reported by Groen and Hemerik (2002) is far higher than their reported minimum value. With their data (assuming that average pre-adult survival equals the mean of first year and adult survival $q = \sqrt{(0.19\ 0.81)}$ our model estimates a yearly population growth rate of 0.88 which implies a yearly decline of about 12%, which is unrealistically strong. Survival data reported by Groen and Hemerik (2002), however, are based on resightings in a local population and the estimate for the survival from fledging to first year is a real minimum as juveniles show lower site fidelity than adults. Published estimates of survival in Black-tailed godwits range from 0.36-0.44 in the first (two) year(s) of life and 0.77-0.95 for adult birds (Roodbergen *et al.* in prep). With average pre-adult survival equal to the mean of first year and adult survival, which range from 0.53-0.65 (based on the data above), and an adult survival value of 0.82 (average of values in Table 1) the number of fledglings per pair (m) required to reach a viable population must range from 0.68-0.83. This value equaled 1.66 when calculated with the survival estimates reported by van Noordwijk and Thomson (2008); this far higher value results from their low adult survival estimate (Table 1). Their survival estimate is, however, based on dead-recovery data only. Survival estimates based on combined dead-recovery and re-sighting data are generally higher because census data on re-sightings contain information that birds had not died (Bressers *et al.* 1991; Klok *et al.* 2006). Given the relatively low values of m reported by Roodbergen and Klok (in press) and adult survival values which are already reasonably high (this value equals 0.93 for the 2nd study; Table 1), we suggest for the declining Black-tailed Godwit populations to focus future management more on reproductive output and pre-adult survival than on adult survival. This suggestion is strengthened by the decline in reproductive output of the species in The Netherlands over the last three decades (Schekkerman *et al.* in press).

Two of the reported data sets for the Curlew suggest population decline for all possible values of pre-adult survival. This is supported by the negative trend in one of the Curlew populations (Grant *et al.* 1999), but not the Curlew population reported by Berg (1991) for which the trend was positive (Table 1). The model estimate for pre-adult survival of the German Curlew population is relatively high compared to published estimates which range from 0.34-0.47 in the first year of life and 0.33-0.63 in the second (Roodbergen *et al.* in prep). Moreover, again adult survival is relatively high in all three populations, therefore we evaluate the elasticity pattern by suggesting a focus of future management on reproduction.

Interestingly, our model results for pre-adult survival in the two Oystercatcher populations, for which complete demographic data and a population trend are given, were higher than those reported in the studies (Table 1). This may partly be a consequence of the fact that our estimate of pre-adult survival (q) is actually the average survival of fledged individuals over the pre-adult lifespan. Reported data in general give estimates of survival in the first year of life (Table 1). If we calculate the

average survival for the pre-adult period assuming that survival of the third to fifth year is equal to the reported adult survival of 0.937, the resulting average pre-adult survival equals 0.729= $(0.5^{2}*0.937^{3})^{1/5}$ which is nearer to our result of 0.77. Based on the elasticity pattern and the scope for increase in the demographic data we suggest a focus on pre-adult survival and reproduction in the case of the population reported by Schankenwinkel (1970) and a focus on adult survival in the case of the population reported by Harris (1967).

The model result for the Redshank implies that either the reported reproduction is an underestimate, or this value stems from a sink population supplemented by immigration. The latter was suggested by (Ottvall, 2005). Given the fact that even if survival of pre-adult and adult individuals is unrealistically high (both > 0.9), populations cannot be viable for the given values of *m*, thus reproduction is a better target for management of this population despite the fact that adult survival has highest elasticity.

In our model we differentiate survival of immature individuals into pre- and post-fledging; pre-fledgling survival is included in the fertility factor (*m*) determining the number of fledglings produced per pair and post-fledging survival appears as (*q*) pre-adult survival in the model. Such a distinction may be violated since chicks are usually ringed at varying ages before fledging, such that reported data on pre-adult survival may partly include pre-fledging survival. If published estimates indeed report both fecundity (as the number of fledged chicks), and pre-adult survival (that includes pre-fledging mortality), the resulting population growth rate estimated with our model can be an underestimate.

Furthermore, we assumed that both pre-adult and adult survival are constant with age. Survival rates may gradually increase over time, both during the immature and the adult stage (Bainbridge and Minton, 1978; Insley *et al.* 1997). The model can be improved by including age-dependent survival. However, data on age-dependent survival rates are largely absent in literature; only three out of 40 literature references on grassland waders reported age-dependent survival (Roodbergen *et al.* in prep.).

Conclusions

As already indicated by Hemerik and Klok (2006) the model framework makes it relatively easy to graphically deduce incomplete demographic data for species. This is a valuable first step for informative management of threatened species, since the framework shows in which part of the parameter space the population is viable ($\lambda \geq 1$). Furthermore, the elasticity graphs show which demographic parameter has the largest influence on the intrinsic rate of population increase. This parameter is the most promising target for management aiming to mitigate population declines, given that this parameter has scope for increase. For the data of the five wader

species, adult survival has the highest elasticity which is a general result for long-lived species (e.g. Heppell *et al.* 1996). Although the demographic parameter with the highest elasticity can in principle be the best target for management (Heppell *et al.* 2000), improvement of this parameter may be restricted if it already has a high value (Norris and McCulloch, 2003). This is illustrated by the published data we report here, which indicate that adult survival is already above 0.8 for nine populations (Table 1). Our result that the elasticity of pre-adult survival (q) increased with time to first reproduction has not been reported previously.

Matrix population models that suggest management decisions by perturbation analysis (sensitivity and elasticity patterns) have been developed for many species, usually case-based and targeting a single species (e.g. Crouse *et al.* 1987; Klok *et al.* 2006). Because endangered species are present in different phylogenetic groups, more general frameworks for setting management priorities are required (Caughley, 1994; Groom and Pascual, 1998). General frameworks have been developed for mammals (Heppell *et al.* 2000) and birds (Sæther and Bakke, 2000; Stahl and Oli, 2006). These compare elasticities between species and show considerable variation in elasticity patterns of closely related species. Our current extension of an earlier model framework (Hemerik and Klok, 2006) differs from the existing ones in that it focuses on the practical applicability for management. It can be used as a diagnostic tool tailored to the available information on groups of species that differ in their age at first breeding.

In our model framework we assumed relatively simple dynamics; all individuals participate in breeding, no density dependence and constant environments (e.g. no stochasticity included). Obviously in the real world not all individuals breed and density dependence and stochasticity can play a role. All these factors tend to depress the yearly population growth rate (Tuljapurkar, 1990; Hemerik and Klok, 2006) which indicates that the missing demographic values inferred from our time-invariant Leslie matrix models are minimal estimates for viable populations. Elasticity patterns, however, seem robust to large changes in parameter values (Caswell, 2000; de Kroon, 2000).

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Appendix

For a life cycle with a pre-adult stage of T years the Leslie matrix has n x n dimensions (where $T+1=n$):

$$Z_n = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & \frac{mq}{2} & \frac{ma}{2} \\ q & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & q & 0 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & 0 & \cdots & q & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & q & a \end{pmatrix} \tag{A.1}$$

The characteristic equation $f_n(\lambda)$ is determined by:

$$\det(Z_n - \lambda I) = 0 \Leftrightarrow f_n(\lambda) = o \quad \text{with} \quad f_n(\lambda) = \lambda^n - a\,\lambda^{n-1} - \frac{mq^{n-1}\lambda}{2} \tag{A.2}$$

The elasticities of the underlying parameters a, q and m of matrix Z_n are easily calculated using implicit differentiation as:

$$e_n(a) = \frac{a\lambda^{n-2}}{f_n'(\lambda)} \tag{A.3}$$

$$e_n(q) = \frac{m(n-1)q^{n-1}}{2f_n'(\lambda)} \tag{A.4}$$

$$e_n(m) = \frac{mq^{n-1}}{2f_n'(\lambda)} \tag{A.5}$$

Where $f'_n(\lambda)$ is used to denote the derivative with respect to λ.
For $n=2$ it holds that $e(m)=e(q)$ and for $n>2$ $e(m)<e(q)$.
To be able to draw the figures 2bc to 5bc we have to determine where the elasticity of the adult survival $e(a)$ equals one of the other elasticities.

First consider $e(a)=e(q)$: this happens when

$$f_n(\lambda)/\lambda = 0 \Leftrightarrow \lambda^{n-1} - a\lambda^{n-2} - \frac{mq^{n-1}}{2} = 0 \text{ and } a\lambda n^{-2} = \frac{m(n-1)q^{n-1}}{2}$$

This results in

$$aq^{n-2}\left(\frac{mn}{2}\right)^{\frac{n-2}{n-1}} = \frac{m(n-1)q^{n-1}}{2} \qquad \text{(A.6)}$$

Now we consider $e(a)=e(m)$: this happens when

$$f_n(\lambda)/\lambda = 0 \Leftrightarrow \lambda^{n-1} - a\lambda^{n-2} - \frac{mq^{n-1}}{2} = 0 \text{ and } a\lambda^{n-2} = \frac{mq^{n-1}}{2}, \text{ this results in}$$

$$aq^{n-2}(m)^{\frac{n-2}{n-1}} = \frac{mq^{n-1}}{2} \qquad \text{(A.7)}$$

Rewriting equations (A.6) and (A.7), we thus have $e(a)= e(q))$ respectively $e(a)= e(m)$ in the (a,q) plane if

$$q = \frac{2}{m(n-1)}\left(\frac{nm}{2}\right)^{\frac{n-2}{n-1}} a \qquad \text{respectively} \qquad q = 2m^{\frac{-1}{n-1}} a$$

For particular values of m and n, both equations are straight lines through the origin. Rewriting equations (A.6) and (A.7) in another way, we have $e(a)=e(q)$ respectively $e(a)=e(m)$ in the (a,m) plane if a as a function of m equals:

$$m = \left(\frac{2a}{q(n-1)}\right)^{n-1}\left(\frac{n}{2}\right)^{n-2} \qquad \text{respectively} \qquad m = \left(\frac{2a}{q}\right)^{n-1}$$

Both equations represent curves through the origin for particular values of q and n.

6 How survival and reproduction in meadow-breeding waders contribute to Europe-wide population changes: review and meta-analysis

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Bert van der Werf
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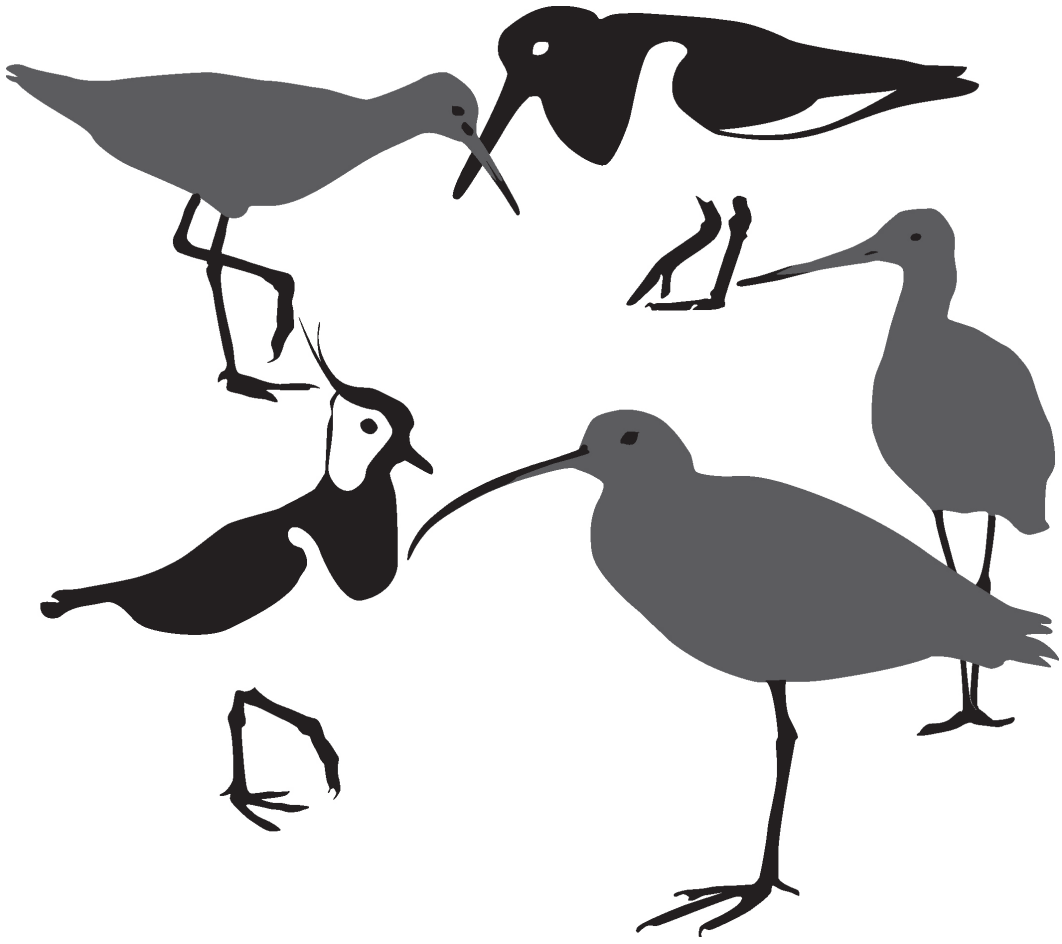
submitted



Abstract

In this review we summarize available data on nest success, chick survival and reproductive output, and adult and juvenile survival of five meadow breeding waders in Europe: Oystercatcher, Lapwing, Black-tailed Godwit, Curlew and Redshank. The assembled studies on survival did not show an overall decline in adult survival in any of these species. However, our meta-analyses on reproduction data show that chick survival declined strongly in the last 40 years in western Europe and that nest success declined in eastern Europe in the period 1995-2005, in Scandinavia in the period 1985-2005, and in western Europe in the period 1950-1980. Predation rates of nests have increased by *c.* +40% in all five species in western Europe during the last four decades. Results on reproductive output, the number of fledglings produced per breeding pair, were less clear-cut. A decline was apparent in Oystercatcher in the period 1963-2005; an initial decline (1953-1990), but slight recent (1990-2006) recovery in Lapwing; an initial decline in Black-tailed Godwit in the period 1985-1995, but again slight increase from 1995 onwards; no trend in Redshank (1992-2006) nor in Curlew (1961-2006). In all five species the results indicate that present population declines are caused by a decrease in reproduction, not in adult survival.

Introduction

Waders breeding in wet grasslands, in this paper referred to as 'meadow birds', are declining rapidly all over Western Europe (BirdLife International 2004b; Teunissen & Soldaat 2006). Breeding habitat deterioration due to urbanization and intensification of agriculture since the 1950s, subsidized by the EU, is considered to be the major factor contributing to this decline (e.g. Chamberlain *et al.* 2000; Donald *et al.* 2001; Gregory *et al.* 2004; Wilson *et al.* 2004; Donald *et al.* 2006). Increased predation of eggs and chicks, due to a combination of increased vulnerability to predation in deteriorated breeding habitat and increased predator densities, may also be an important factor (Bellebaum 2003; Langgemach & Bellebaum 2005; Bolton *et al.* 2007; Teunissen *et al.* 2008; Schekkerman *et al.* 2009). Another threat for the near future is the intensification of rice farming at stop-over sites (Kuijper *et al.* 2006; Lourenço & Piersma 2008).

Agricultural intensification in breeding areas will mostly affect reproduction, while other types of habitat destruction may affect both reproduction and survival, by reducing the area of suitable breeding and foraging habitat. Increased predation of eggs and chicks also mainly affects reproduction, but may in addition decrease adult survival if incubating adults are taken, or if replacement clutches are produced at the expense of adult survival. Most authors agree that present population declines in meadow birds are expected to be mainly caused by a decrease in reproduction (Kruk *et al.* 1997; Roodbergen & Klok 2008; Schekkerman 2008; King *et al.* 2008), but survival may also have declined (e.g. Van Noordwijk & Thomson 2008).

Data on temporal trends in demographic parameters are necessary to diagnose the population decline. The results of such a diagnosis can help to choose effective conservation measures. Most demographic studies of meadow birds focus on local trends and underlying demographic parameters, while little is known on mechanisms behind international trends. Though local conditions may vary greatly, large-scale processes such as agricultural intensification or climate change are likely to affect vast areas and therefore large-scale studies are badly needed. Moreover, many, if not most, local studies are only published in the grey literature, which is difficult to access for researchers and policymakers.

Here we collated and analyzed available studies on reproduction and review literature on survival in five meadow bird species: Oystercatcher (*Haematopus ostralegus*), Northern Lapwing (*Vanellus vanellus*), Black-tailed Godwit (*Limosa limosa*), Eurasian Curlew (*Numenius arquata*) and Redshank (*Tringa totanus*). All five waders are to a large extent dependent on agricultural grasslands and show a moderate (>10%, Oystercatcher, Curlew, Redshank) to large decline in Europe (>30%, Lapwing, Black-tailed Godwit, BirdLife International 2004a).

Materials and methods

Data on reproduction

We compiled data from scientific literature, from 'grey' reports and unpublished studies including own data (see Hötker *et al.* 2007), and extracted the following parameters:

(1) nest success (proportion of clutches in which at least one egg survives to hatching), including proportion of clutches lost due to agricultural activities and predation, (2) survival rate of chicks (percentage of chicks surviving from hatching to fledging) and (3) reproductive output (number of chicks fledged per breeding pair).

Nest success

Nest success was given per study area per year and was either calculated by dividing the number of successful clutches by the number of clutches found ('classical method', used in 323 records) or by methods based on daily survival rate estimates (e.g. Mayfield 1975; Aebischer 1999, used in 319 records). When clutches have not been monitored from the onset of laying, the classical method overestimates nest success, while methods based on daily survival rate estimates are unbiased (Green 1989). 'Classical' nest success was therefore converted to 'Mayfield' nest success using the correction factors proposed by Hötker (2010). The proportions of clutches lost due to predation or agricultural activities, if not directly given by the authors, were calculated as the proportion of the total number of nests that was lost to the given cause (if applicable after conversion to unbiased nest success). Proportions of nests lost to all different causes therefore add up to the absolute proportion of unsuccessful nests (for more details see Hötker 2010). This calculation could not be performed with many of the older data; these data were therefore discarded. Losses due to agriculture included losses due to trampling by cattle or sheep. Clutches having disappeared by unknown causes were regarded as being predated.

Chick survival

Like nest success, chick survival was reported to have been measured in different ways. In some cases, chicks or parents marked with rings or radio-transmitters were followed individually. In most cases however, chick survival was estimated by dividing the mean number of fledglings present at a study site by the mean number of chicks hatched (taken from data on hatching success).

Reproductive output

Data on reproductive output were used as reported in publications or by researchers. Most of the data were obtained by simple counts of alarming pairs, i.e. counting the number of broods with fledglings and multiplying this number with the mean brood size at fledging. Few studies were based on marked or radio-tagged individuals.

Not all species were studied at all sites and over the same period, and not all parameters estimated in each study. Sample sizes varied accordingly. We omitted data on nest success, chick survival or reproductive output based on sample sizes smaller than five clutches or pairs per site and year combination. Only data from grassland and arable land were included. Altogether 1460 site year combinations from the period 1948-2006, including estimates of at least one of the parameters nest success, chick survival and reproductive output, were collected from the following countries: Western Germany (1134), Eastern Germany (43), The Netherlands (86), Denmark (82), UK (58), Switzerland (45) and Sweden (12). These countries were grouped in three different agricultural regions, based on the degree and timing of agricultural intensification (see Donald *et al.* 2001): eastern Europe (Eastern Germany), western Europe (Western Germany, The Netherlands, UK, Switzerland) and Scandinavia (Denmark, Sweden). Whenever we use the terms eastern Europe, western Europe and Scandinavia we refer to these agricultural regions.

Statistics

When assembling data from many different sources, unbalanced data structures and differences in methodology are bound to diminish the comparability of the data collected and to complicate analyses. We tried to accommodate for these problems by including methodology as a factor in the analyses, by only analyzing sufficiently large sample sizes and applying weights, and by using mixed models, which are especially suited for meta-analyses (Payne R.W. *et al.* 2008).

We used generalized linear mixed models (GLMM) in Genstat (11th edition) to analyze whether the available reproductive parameters changed over time. The binomial distribution with logit-link function was used for all percentages, with 100% as binomial totals and a free dispersion parameter. Reproductive output was given as the number of fledglings per breeding pair and was log-transformed, after adding 0.5 to the values, to obtain data not deviant from normality. In the analyses of chick survival and reproductive output, the square root of the sample size (number of pairs studied) was included as a weight factor. If no data on sample size were present, the median sample size was inferred. Fixed terms included in the models were: method of data collection for chick survival and reproductive output (with two levels: 1. rings/radio-telemetry and 2. counts of alarming pairs), species, year, year^2 and the interaction of species with year and of species with year^2. Only few data were available from the agricultural regions eastern Europe and Scandinavia. Therefore the factor 'agricultural region', and its interaction with year and year^2 was only included where sample sizes allowed for this. If not, only data from western Europe were included. Site was included as a random factor to correct for site effects. We determined the best models for all five reproductive parameters by backward selection using Wald statistics and $\alpha = 0.05$. Whenever an interaction was significant, the main effects were also included in the model.

Survival

In early survival analyses, estimates of (age-dependent) mortality rates were calculated from the age distribution of birds recovered dead or, in the case of live recaptures or resightings, as the return rate (number resighted at t+1 / number alive at t) (Lack 1954, Grosskopf 1964). To account for birds that are still alive at the end of the study, Haldane (1955, in Grosskopf 1964) developed a correction for the first type of analysis. These methods, referred to as 'old' methods in our paper, do not consider variations in probabilities of dead birds being reported or live birds being resighted or recaptured. As these variations can be considerable, old methods often give unreliable (and usually too low) survival estimates.

In the 1970s, more sophisticated methods, referred to as 'new' methods in our paper, were developed by Seber (1970) for dead recoveries, estimating both reporting and survival rate and Cormack (1964), Jolly (1965) and Seber (1965) for live recaptures, estimating both resighting rate and apparent survival. However, also in new methods, heterogeneity in reporting rates may complicate analyses of data on dead recoveries, while in studies using live recaptures only, no distinction can be made between permanent emigration and mortality; resulting survival estimates therefore represent apparent (local) survival. Apparent survival will typically be lower than true survival, the error increasing with decreasing site fidelity of the birds studied.

Survival estimates based on dead recoveries and/or live recaptures/resightings may generate different outcomes (Francis & Cooke 1993). The scale at which dead recoveries are collected is typically larger in time and space (country or species range) than the scale at which live recaptures are assembled (study area).

The different methods used complicate comparisons between studies, especially because methods change through time, and such comparisons should therefore be made with care. Heterogeneity and scarcity of data did not allow for statistical analyses. All studies concerning data before 1977 used old methods of analysis. We included such studies in the species-specific tables on survival (appendix A-E) for completeness, but in the text we only discuss estimates based on 'new' methods of analyses.

Results

Meta-analysis of data on reproduction

Mean values for the five reproductive parameters in western Europe for all species in the periods '<1981', '1981-1995' and '1996-2006' can be found in table 1. The best models for the five reproductive parameters, together with significance levels of the variables included, are given in table 2. Here, we only discuss the trends and correlations that proved significant, unless stated otherwise.

Table 1. Mean parameter values with number of studies (N) and standard errors for five meadow bird species in western Europe in the periods '<1981', '1981-1995' and '1996-2006'. N.a. = not available. Oyst: Oystercatcher, lapw: Northern Lapwing, btg: Black-tailed Godwit; curl: Eurasian Curlew, reds: Redshank.

period		<1980			1981-1995			1996-2006		
	Species	N	Mean	s.e.	N	Mean	s.e.	N	Mean	s.e.
nest success (%)	oyst	9	36.49	4.27	4	16.85	6.55	26	47.52	3.70
	lapw	65	43.39	2.51	71	38.34	2.43	128	32.10	1.76
	btg	3	34.86	13.59	47	35.98	2.77	96	36.42	2.30
	curl	3	38.08	8.22	23	25.99	3.04	43	29.51	2.60
	reds	2	45.72	32.12	5	36.80	10.04	18	34.29	6.54
Predation of nests (%)	oyst	6	38.97	4.65	4	41.75	19.94	8	48.02	8.39
	lapw	19	17.94	2.87	45	30.80	3.88	52	56.31	3.93
	btg	n.a.	n.a.	n.a.	19	21.34	4.21	24	42.11	5.72
	curl	3	16.49	5.91	11	52.73	10.03	1	65.00	n.a.
	reds	2	46.00	25.00	3	3.37	1.70	3	56.31	24.92
Nest losses due to agricultural activities (%)	oyst	6	11.13	6.94	4	41.40	21.74	8	5.90	2.46
	lapw	19	11.77	2.84	45	16.20	2.16	52	9.63	1.88
	btg	n.a.	n.a.	n.a.	19	22.53	5.03	24	14.07	3.74
	curl	3	18.95	13.05	8	17.88	6.29	n.a.	n.a.	n.a.
	reds	n.a.	n.a.	n.a.	3	59.29	16.47	3	5.58	2.80
Chick survival (%)	oyst	5	49.00	5.52	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	lapw	27	51.62	6.59	18	21.13	2.13	31	21.26	2.72
	btg	n.a.	n.a.	n.a.	4	33.00	3.40	19	16.00	3.46
	curl	7	29.86	4.77	1	23.00	n.a.	3	49.00	6.08
	reds	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	1	80.00	n.a.
Reproductive output (no. fledglings per breeding pair)	oyst	9	1.11	0.09	12	0.20	0.05	12	0.24	0.09
	lapw	29	0.75	0.12	70	0.50	0.06	162	0.40	0.03
	btg	n.a.	n.a.	n.a.	100	0.47	0.04	173	0.41	0.03
	curl	36	0.40	0.11	201	0.37	0.03	250	0.34	0.02
	reds	n.a.	n.a.	n.a.	5	0.62	0.10	33	0.34	0.06

Nest success

Nest success declined strongly in all species in eastern Europe and Scandinavia, from *c.* 40% in the mid-1990s to *c.* 20% around 2000 in eastern Europe and from *c.* 70-80% in the 1980s, to *c.* 30% in 2006 in Scandinavia. It also declined in western Europe, from over 50% to *c.* 40%, but seems to be slightly increasing again since the 1980s (table 2 and fig. 1). Nest success did not differ significantly between species. Only after 1983 data are available for all species and all agricultural regions. However, the pattern and level of significance (table 2) remain valid when data before 1983 are excluded.

Table 2. The most parsimonious models for the five reproductive parameters. N is the sample size per agricultural region (eEu: eastern Europe, Sc: Scandinavia, wEu:western Europe). Data on chick survival and reproductive output have been collected in two different ways: by counting alarming pairs (C) or by following individual families using rings and/or radio-telemetry (R). Data given between brackets were not included in the models. N.a.: not available.
** p<0.05, ** p<0.01, *** p<0.001, n.s.: none of the variables significant (mixed effects models, Wald test for dropping variable from model).*

Reproductive parameter		N eEu	N Sc	N wEu	model
Nest success		12	87	543	constant+region+year+year^2+region.year*+region.year^2*
Predation losses		(1)	(12)	199	constant+species*+year*+year^2*
Agricultural losses		(1)	(5)	194	constant+year**+year^2**
Chick survival	C	n.a.	(3)	85	constant+year***
	R	n.a.	(4)	31	
Reproductive output	C	35	7	1059	constant+species*+year+year^2+species.year***+species.year^2****
	R	0	4	33	
Oystercatcher	C	n.a.	n.a.	33	constant+year**
	R	n.a.	n.a.	n.a.	
Lapwing	C	16	7	253	constant+method**+year**+ year^2**
	R	n.a.	n.a.	8	
Black-tailed Godwit	C	(3)	n.a.	249	constant+method+year+method.year***
	R	n.a.	n.a.	24	
Curlew	C	(11)	n.a.	487	n.s.
	R	n.a.	n.a.	n.a.	
Redshank	C	(5)	n.a.	37	constant+year*
	R	n.a.	(4)	(1)	

Predation rates of nests have significantly increased by *c.* +40% in all five species in western Europe during the last four decades (table 2 and fig. 2). Predation rates were highest in Curlew and Oystercatcher and lowest in Black-tailed Godwit. In western Europe, nest losses due to agricultural activities have significantly increased from *c.* 10% in the 1960s to *c.* 20% in the 1980s, but decreased again to below 10% after 2000, regardless of species (table 2 and fig. 3).

Chick survival
Chick survival declined linearly from over 40% in the 1960s, to *c.* 20% after 2000 in western Europe, irrespective of species (table 2 and fig. 4)

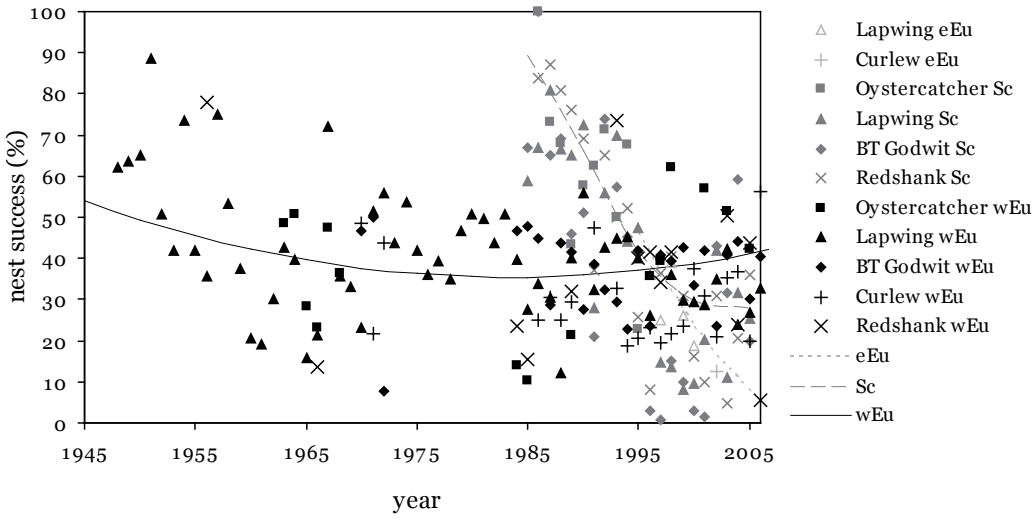


Figure 1. Nest success in five species of meadow birds in three agricultural regions. The graphs are back-transformed predictions from the best model; data are given as yearly means. eEu: eastern Europe; Sc: Scandinavia; wEu: Western Europe.

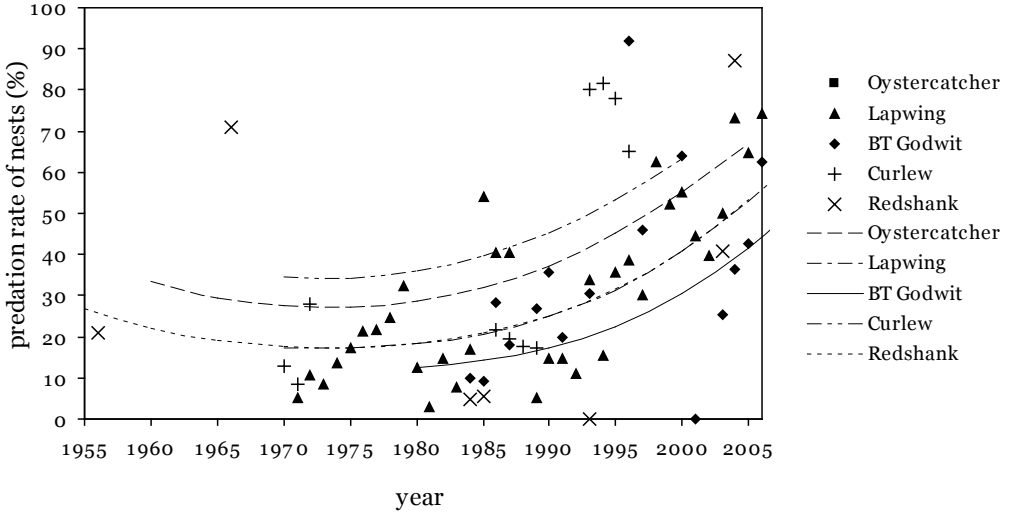


Figure 2. Predation rate of nests in five species of meadow birds in western Europe. The graphs are back-transformed predictions from the best model; data are given as yearly means.

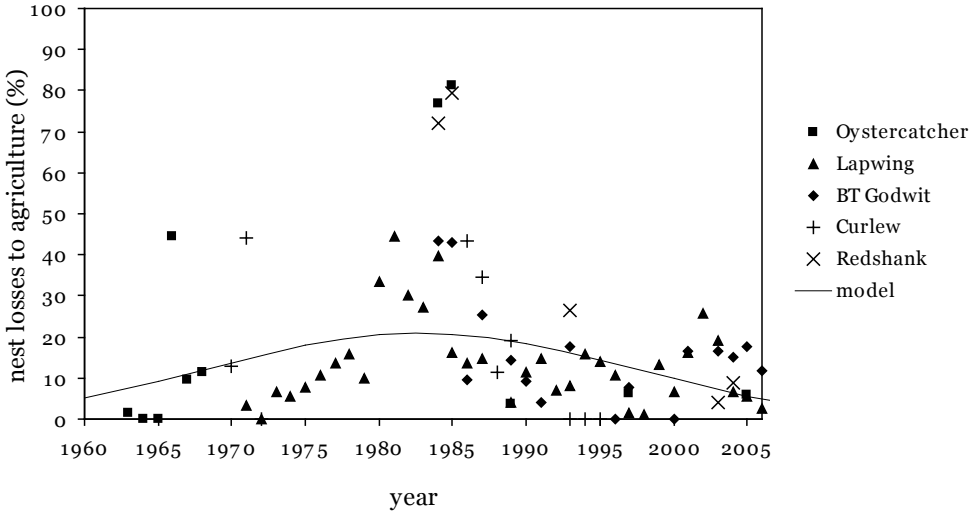


Figure 3. Nest losses due to agricultural activities in five species of meadow birds in western Europe. The graph represents back-transformed predictions from the best model; data are given as yearly means

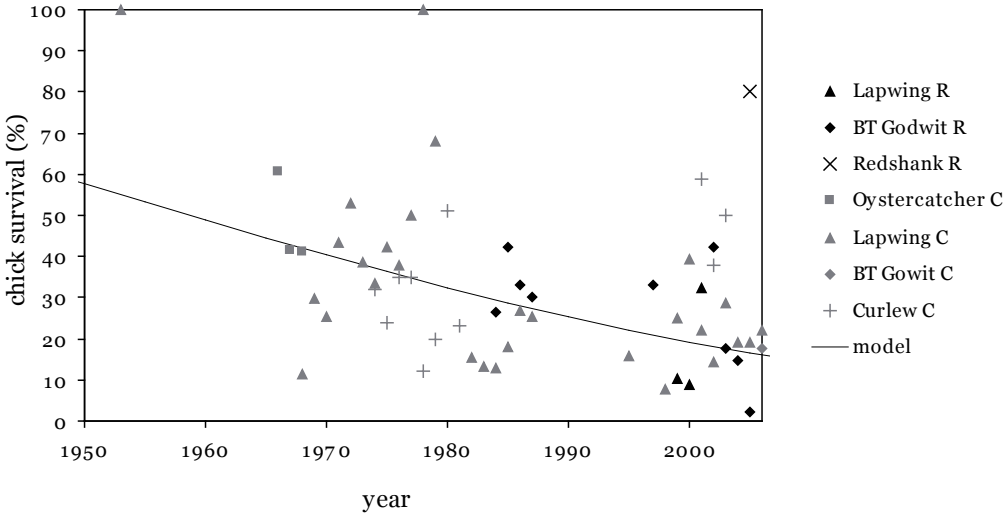


Figure 4. Chick survival in five species of meadow birds in western Europe. R: (color) rings and/or radio-telemetry, C: counts of alarming pairs. The graph represents back-transformed predictions from the best model; data are given as yearly means.

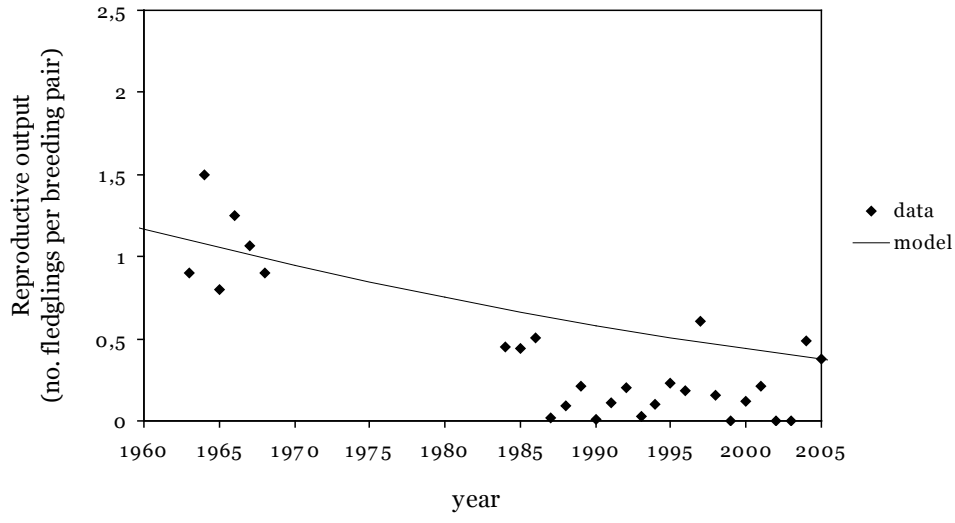


Figure 5. Reproductive output in Oystercatcher in western Europe. The graph represents back-transformed predictions from the best model; data are given as yearly means

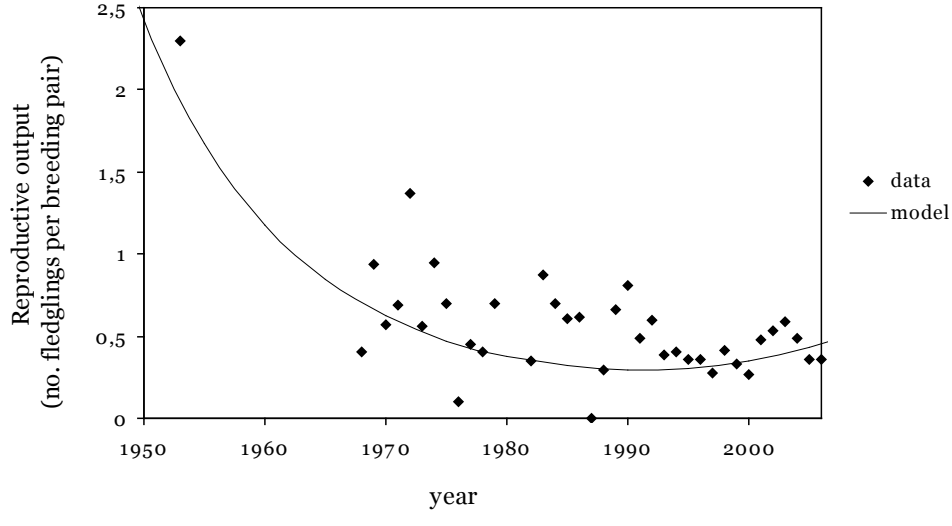


Figure 6. Reproductive output in Lapwing. The graphs represent back-transformed predictions from the best model; data are given as yearly means.

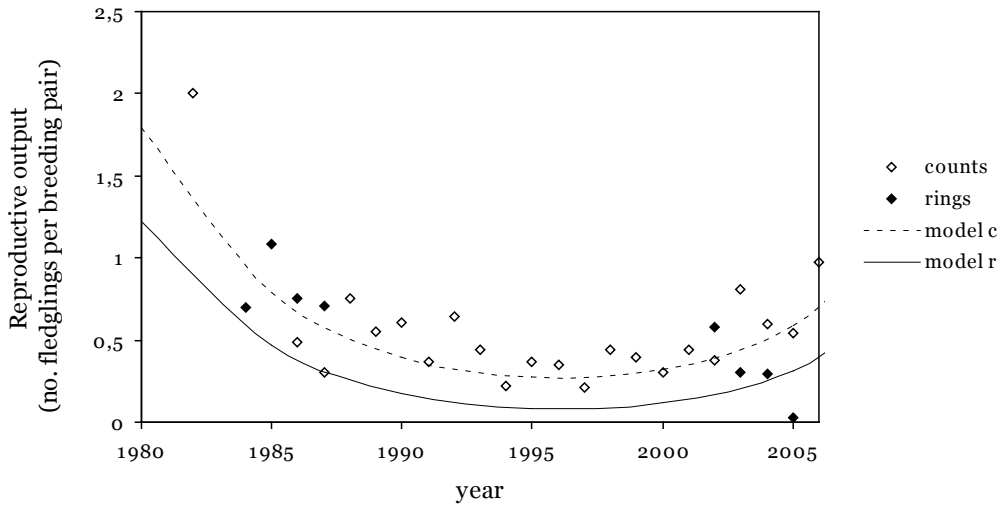


Figure 7. Reproductive output in Black-tailed Godwit in western Europe. Rings & R: data collected using (color) rings and/or radio-telemetry, counts & C: data collected by counting alarming pairs. The graphs represent back-transformed predictions from the best model; data are given as yearly means.

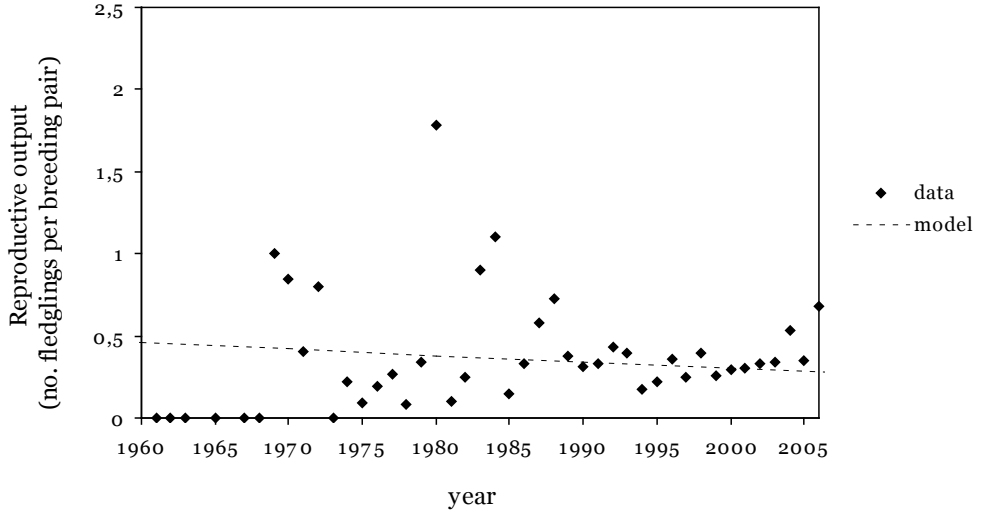


Figure 8. Reproductive output in Curlew in western Europe. The graphs represent back-transformed predictions from the best model (intermittent line). However the model was not significant (p=0.081). Data are given as yearly means

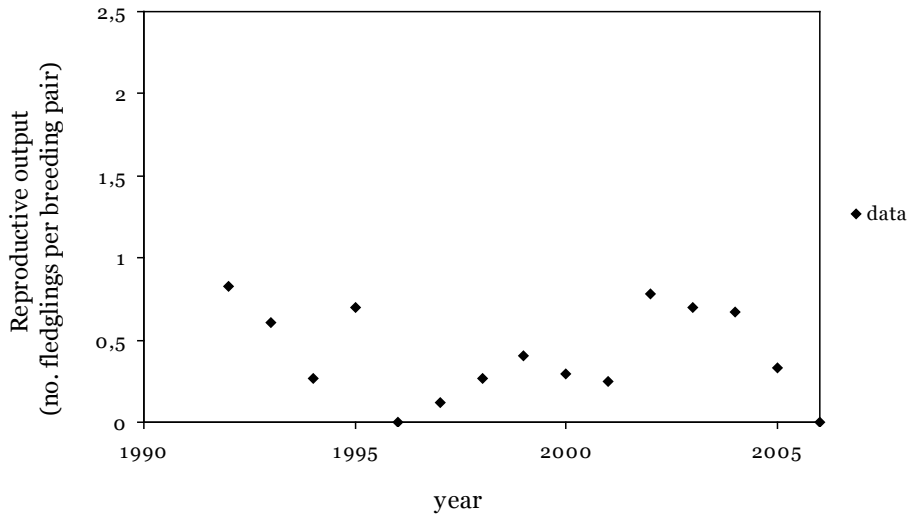


Figure 9. Reproductive output in Redshank in western Europe. No model could be fitted to the data. Data are given as yearly means.

Reproductive output

In models for reproductive output, the interactions between species and year and between species and year^2 were significant, therefore each species was also tested separately (table 2). Agricultural region did not have a significant effect on reproductive output. In Oystercatchers in western Europe, reproductive output declined linearly from *c.* 1 young fledged per breeding pair in the mid-1960s to below 0.5 after 2000 (fig. 5). Reproductive output also declined in Lapwing, from *c.* 0.7 in the 1970s to *c.* 0.3 in the 1990s, regardless of agricultural region, but seems to have stabilized or even slightly increased afterwards (fig. 6). However, the high value in 1952 is likely to have a large effect on the outcome of the analyses A similar trend but in a different period can be found in the Black-tailed Godwit in western Europe (fig. 7): a decline from *c.* 0.7 fledglings per breeding pair around 1985 to *c.* 0.2 in the mid 1990s, followed by a slight increase to *c.* 0.4 around 2005. Data collected using ringing and/or radio-telemetry show significantly lower values than data collected by counting alarming pairs, though of the first only few data are available (24 vs 249, table 2), with no data from the 1990s. Reproductive output in Curlew declined slightly since the 1970s, but this decline was not significant, possibly due to repeatedly low values in the 1960s (fig. 8). In Redshank, data on reproductive output were only present after 1992. The data did not show a trend with year or year^2 (fig. 9).

Survival review

Oystercatcher
Many data are available on survival estimates in Oystercatchers (appendix A), but only one (recent) study specifically focused on inland breeding birds (Bruinzeel *et al.* 2009). This study was based on Dutch national ringing recoveries and found higher survival rates in inland ringed Oystercatchers than in coastal breeding birds in all age classes during the non-breeding season and in (sub)adults during the breeding season. Yearly survival rate estimates were 0.18 for juveniles, 0.96 for subadults and 0.92 for adults. This study also found a decrease in juvenile survival rates during the non-breeding season (mid-July to mid-March), from c. 0.4-0.5 in the 1960s to c. 0.1 in recent years. The non-breeding season in juveniles in this study was defined as the period from the moment of ringing until the next breeding season and thus included part of pre-fledging mortality, which implies that a decrease in juvenile survival might be (partly) caused by decreased reproduction. In some studies, estimates for adult survival also decreased (Neve & Van Noordwijk 1997; Le V.Dit Durell *et al.* 2000; Oosterbeek *et al.* 2006). However, two of these were carried out in the Dutch Wadden Sea area and according to Bruinzeel *et al.* (2009) these are mostly coastal breeding birds. The third study was carried out in the Exe estuary, where the wintering population was increasing and winter mortality was found to be density dependent in mussel feeding birds. However density dependent mortality cannot explain trends in decreasing populations.

Lapwing
When only more recent studies using new methods are considered, adult survival rate estimates in Lapwing ranged from 0.75 to 0.83 and first year survival from 0.23 to 0.63 (appendix B). Bruinzeel (2009) found an increase in juvenile survival from less than 0.2 in the 1960s to over 0.3 around 2000, while Peach *et al.* (1994) found an increase in adult survival, though this was not confirmed by more recent analyses of more extensive data sets, including the same data (Catchpole *et al.* 1999; Besbeas *et al.* 2002; King *et al.* 2008; Sharpe *et al.* 2008). Rather, Catchpole *et al.* (1999) and King *et al.* (2008) show that recovery rates have declined during the study period. None of the other studies give trends in adult survival. Using ring recovery data and population models, Besbeas (2002) and King *et al.* (2008) show that the population decline of Lapwings in England is most likely caused by a decreased reproduction, not survival.

Black-tailed Godwit
All studies on the subspecies *limosa* using new methods of analyses were carried out in The Netherlands. Estimates of juvenile survival varied between 0.36 and 0.4 and of adult survival between 0.7 and 0.95 (appendix C). Van Noordwijk and Thompson

(2008) argue that adult survival rates have declined between 1995 and 2000, but the precision of this estimate is low due to declining sample sizes and falling reporting rates. Rather, according to a more recent study based on the same data plus data from recent years (Bruinzeel *et al.* 2009, 1959-2008 vs 1960-2000), adult survival in Dutch Black-tailed Godwits even increased from 0.7 in the 1960s to 0.8 in the last 30 years, due to an increase in survival during the non-breeding season. The authors give several explanations for this increase: 1) a decrease in hunting pressure, 2) a change in use of stop-over and wintering areas, possibly related to an increase in rice production, 3) a decrease in competition, and last but not least 4) a trade-off with reproduction, so that a decrease in reproduction might cause an increase in adult survival rates. It is also worthwhile noting that some recent estimates on adult survival in *limosa* fall in the range of estimates on adult survival in the increasing Icelandic subspecies, *islandica*, suggesting that the present decline in *limosa* is not caused by a decrease in adult survival.

Curlew

Recent data (>1992) on Curlew survival are lacking, which in this case also means there are no reliable survival data, as the available studies are all based on old methods of analysis. Adult survival estimates vary between 0.72 and 0.89, those for second year birds between 0.33 and 0.63 and for first year birds between 0.34 and 0.47 (appendix D). Adult survival estimates in the period after the mid1970s based on return rates tend to be higher (1973-1992; 0.82-0.89) than those based on older ringing-recovery data (1909-1975; 0.72-0.75), but no conclusions can be drawn on trends in survival due to insufficient (comparable and reliable) data.

Redshank

Only two studies on survival in Redshank consider populations breeding on meadows (Ottvall 2005; Bruinzeel *et al.* 2009). These give an estimate for juvenile survival of 0.53 and of adult survival of 0.77-0.80 (appendix E). As in the Oystercatcher, juvenile and adult survival in the Netherlands was higher in inland breeding than in coastal breeding Redshank (0.39 and 0.74 respectively). However, this difference was not significant and the estimates for adult survival are comparable to those in coastal populations (0.72-0.93). Insley *et al.* (1997) found that survival in Redshank increased with age, from 0.43 in second calendar year Redshank, varying greatly between years (from 0.06 to 0.84), to 0.67 in third calendar year and 0.74 in older Redshank. As captures were carried out in winter, no chicks were ringed and first year survival could not be estimated. No trends were found in either adult or juvenile survival estimates, except for the study in the Exe estuary (Burton *et al.* 2006), where adult survival declined due to closure of a barrage, which considerably decreased available habitat. The same study noted a simultaneous increase in survival in Northern Wales, which had nothing to do with the closure

Discussion

Though comparing and analyzing data from different sites, periods and species and collected using different methods remains problematic and therefore care should be taken in drawing firm conclusions, such analyses can give valuable insight into large-scale processes. In this case we analyzed reproductive data with a maximum time span of 58 years, from seven different countries, differing in degree and timing of agricultural intensification. Our results support the notion that declines in meadow birds are caused rather by decreased reproduction than by decreased adult survival.

Reproduction

Nest success declined in all three agricultural regions, though it seems to have stabilized and even to be slightly increasing again in western Europe. This could partly be explained by nest protection, which is more commonly practiced in western Europe. However, this may give a too optimistic picture, as areas with nest protection are probably over represented in the dataset (see below). Nest success declined more strongly in eastern Europe and Scandinavia, but sample sizes from these regions are smaller and often come from only few areas. According to Gregory *et al.* (2005), numbers of farmland birds increased in central eastern Europe after the collapse of agriculture in 1990. However, both Reif *et al.* (2008), and Zidkova *et al.* (2007) show that in the Czech republic farmland species, amongst which Lapwing, declined during the period of intensification, but continued to do so after the collapse of agriculture in 1990, which Reif *et al.* (2008) explain by a simultaneous decrease in the area of arable land. This is supported by Wretenberg *et al.* (2007), who suggest that extensification is beneficial to farmland birds, but that in regions of low agricultural profitability and an already ongoing extensification, a further extensification will lead to loss of both farmland habitat and bird diversity.

We found predation rates to have increased over the last 40 years in western Europe. Though we may have overemphasized the role of predation by regarding clutches having disappeared from unknown causes as being predated, we expect this bias to be small, as the proportion of these clutches is small. In many European countries densities of predators of ground nesting birds have increased (Panek & Bresinski 2002; Bellebaum 2003; Teunissen *et al.* 2005; Langgemach & Bellebaum 2005), though good data on predator densites are scarce. This is attributed to changes in landscape features, such as lowering of water tables, reduction of landscape openness and changes in agricultural practices (Langgemach & Bellebaum 2005), though in the case of the Red Fox *Vulpes vulpes*, changes in hunting practices and eradication of rabies may also have played a role (Panek & Bresinski 2002; Bellebaum 2003). Note, however, that many data on nest success originate from areas with nest protection and/or management agreements or from nature reserves. Especially the latter may

be areas that are also more attractive to predators, due to higher prey densities and more cover. Moreover, protection of nests as practiced in The Netherlands may also unintentionally increase predation rates, by creating olfactory or visual tracks to nests and disturbing breeding birds (Goedhart *et al.* 2010). More importantly, this bias towards protected and less intensively managed areas may explain the decline in nest losses due to agricultural activities since the early 1980s. This coincides with the period when the first management agreements aimed at conservation of meadow birds were signed. It is likely that the percentage of nests lost to agricultural activities, which started to increase in the mid 1960s when populations of meadow birds peaked, continued to do so in unprotected areas. Indeed, Teunissen *et al.* (2008) show that losses due to agriculture in The Netherlands increased from the late 1980s to the late 1990s in areas without nest protection. This bias might also explain the slight increase in nest success in western Europe since the 1980s.

The analyses show a negative trend in chick survival in the past four decades. No significant differences between species were found, which can partly be explained by the unbalanced structure of the data (Redshank: n=1, Oystercatcher: n=5, Curlew: n=11, Black-tailed Godwit: n=23 and Lapwing: n=76). However, though families with chicks of the five species to some extent differ in habitat preference, in western Europe all five species are faced with habitat deterioration due to intensification of agriculture. In addition, as predation rates of nests have increased, predation rates of chicks may also have increased. Moreover, intensification of agriculture may enhance predation as large- scale mowing removes cover and chicks may need to travel larger distances and take greater risks due to lower food availability. Finally, climate change may influence the timing of the peak in food abundance, which may in turn cause a mismatch between timing of breeding and optimal conditions for reproduction (Visser *et al.* 1998; Both & Visser 2001; Roodbergen & Klok 2008; Schroeder 2010).

Trends in reproductive output are less unambiguous: a decline in Oystercatcher; an initial decline but slight recent increase in Lapwing and Black-tailed Godwit; no trend in Curlew and Redshank. The bias towards protected and less intensively managed areas as discussed above may also influence trends in reproductive output. Furthermore, the differences in methodological approaches between studies and the inaccuracy of some methods may have obscured trends in the data. Only few studies used color rings and/or radio transmitters to follow individual chicks or families. The majority of data are based on simple observations, which give a very crude measure of chick survival or reproductive output. Without individual recognition of families, results will inevitably be influenced by replacement clutches, double counting, or focusing on alarming and thus probably successful pairs. Therefore, though the range of estimates seems realistic, the estimates of chick survival and reproductive output presented in this paper should be treated with care and rather be considered as an index to compare trends than as an absolute value.

Survival

Reliable data on adult and especially juvenile survival are scarce. Differences between old and new methods of analysis and between live recaptures and dead recoveries may obscure trends in survival. Three of the five species (Oystercatcher, Curlew and Redshank) frequently breed in other habitat than agricultural grasslands and most survival estimates are based on these individuals. Though all individuals probably mix at the stop-over and wintering sites, survival between individuals breeding in (semi-)natural habitats and those breeding in agricultural grasslands may differ, as showed by Bruinzeel *et al.* (2009). Another problem with survival studies in general is that most birds are ringed in areas where they occur in high numbers, which are often also areas of better quality habitat. As with reproduction, survival may be higher in good quality habitat than in sites of lesser quality (Gill *et al.* 2001).

There is no clear indication in any of the species of a general decrease in adult survival over the past 30 years, though there are problems with the comparability of the data. Data on juvenile survival are too scarce to allow for any conclusions.

Conclusions and recommendations

This study is the first to summarize available data on reproduction and adult and juvenile survival of five meadow breeding waders. Our results indicate that there is no overall decline in adult survival in any of the species, but that chick survival declined strongly in the last 40 years. Nest success declined in eastern Europe and Scandinavia, and initially but not recently in western Europe. Trends in reproductive output were less straightforward, but present reproductive output is likely too low to compensate for mortality. This is probably even more true in lower quality habitat, which is almost certainly underrepresented in the data.

Predation rates of nests increased in all five species. For effective conservation measures it is important to know the reason for this increase. More studies on the interaction of management and predation and on predator densities are needed.

In Black-tailed Godwit, reproductive output estimated from counts of alarming pairs were more optimistic than those estimated using color rings or radio-telemetry. We recommend using the latter methods to estimate chick survival and reproductive output, as these are likely to give more reliable results. However, they are more time consuming and expensive, which usually implies low sample sizes. The alternative, counting alarming pairs, therefore seems attractive, but should be evaluated and calibrated using the aforementioned methods, before further implementation.

Historical and recent survival estimates are not readily comparable. Statistical reanalyses of historical survival data using new methods are needed to discover

trends in survival. The large variation in reproductive parameters and survival rates argues for more long-term population studies estimating both reproduction and juvenile and adult survival at the same site. More effort should also be put into distinguishing pre- and post-fledging survival, as estimates on juvenile survival are biased low due to pre-fledging mortality, which is already included in estimates of reproductive output. Finally, for population models more data on the proportion of adults that start breeding are badly needed, together with the occurrence of replacement clutches and data on dispersal, immigration and emigration.

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Appendix A

Adult (a) and juvenile (j, first year) survival estimates of Oystercatcher.

site	habitat[a]	period	method[b]	j survival[c]	a survival[d]	surv.trend[e]	pop.trend[e]	source
Netherlands	M	1959-2008	L+D	0.18	0.96 (sa), 0.92 (a)	j nb season -	-	1
Netherlands	C+M	1959-2008	L+D	0.18 (C), 0.21 (M)	0.74 (sa, C), 0.81 (sa, M) 0.86 (a, C), 0.89 (a, M)		-	1
England Exe estuary	C	2002-2006	L(r)		0.91 m, 0.84 f	0	-	2
Netherlands Texel	C+M	1984-2005	L		0.88	0	- < 2000, 0/+ > 2000	3
Netherlands Schiermonnikoog	C	a 1984-2005, j 1984-2002	a L, j D	0.55	0.93	a -, j 0	-	3
Netherlands Schiermonnikoog	C	a 1985-2004, j 1985-1996	a L, j D	0.44 (low quality habitat) 0.61 (high quality habitat)	0.73 (2nd y) 0.97 (3rd y) 0.87 (a low quality habitat), 0.81 (a high quality habitat)	0	-	4
Wales Traeth Lafan	C(+M?)	1980-2003	D		0.91	0	- late 1980s, + 2000-2002	5
Netherlands Delta	C	1981-2001	L		0.99 mild winters Oosterschelde 0.55-0.99 severe winters Oosterschelde 0.84-0.90 mild winters Westerschelde + Haringvliet 0.37-0.76 severe winters Westerschelde + Haringvliet			6
England Wash	C	1968-1998	D		0.89	0	+ < 1988, - > 1988	7
Netherlands Wadden Sea	C(+M?)	1980-1996	L+D	0.28	0.65 (2nd cy), 0.85 (> 2nd cy)	-	-	8
Netherlands Schiermonnikoog	C	1985-1991	L(r)	0.53				9

Appendix A continued

site	habitat[a]	period	method[b]	j survival[c]	a survival[d]	surv.trend[e]	pop.trend[e]	source
England - Exe estuary	C(+M?)	1976-1991	L		0.89	-	+	10
Netherlands Schiermonnikoog	C	1983-1989	L(r)		0.90			11
Wales - Skokholm	C	1964-1977	L(r)		0.90	0	0	12
Wales - Skokholm		1963-1969	L(r)		0.92	0	0	13
Germany - Mellum	C	1949-1962	L(r)	0.5 (1st & 2nd cy)	0.94	0	+ < '65, 0 > '65	14
Netherlands	C+M	1925-1956	D(Lack)	0.64	0.84			15
Germany	C	1949-1955	L(r)		0.93			16
Sweden & Norway	C	<=1954	D(Lack)		0.70			15
Germany	C	1949-1953	L(r)		0.86			17
Denmark	C(+M?)	1920-1946	D(Lack)		0.74			15

Abbreviations:

a) C = coastal, M = meadow, A = arable, H = heather

b) L = live resightings, (r) = return rate only, not corrected for resighting probability, D = dead recoveries, (Lack) or (Haldane)= Lack's or Haldane's method, not corrected for reporting probability

c) j = juvenile, b = breeding, nb = non-breeding

d) a = adult, sa = subadult

e) - = decrease, 0 = stable, + = increase, no value = not given

Literature:

1) Bruinzeel et al. 2009, 2) Le V.Dit Durell 2007, 3) Oosterbeek et al. 2006, 4) van de Pol et al. 2006, 5) Atkinson et al. 2005), 6) Duriez et al. 2009, 7) Atkinson et al. 2003, 8) Neve & Van Noordwijk 1997, 9) Kersten & Brenninkmeijer 1995, 10) Le V.Dit Durell et al. 2000), 11) Hulscher 1989, 12) Safriel et al. 1984, 13) Harris 1970, 14) Schnakenwinkel 1970, 15) Boyd 1962, 16) Grosskopf 1964), 17) Jungfer, 1954 in (Boyd 1962)

Appendix B

Adult (a) and juvenile (j, first year) survival estimates of Lapwing.

country	habitat[a]	period	method[b]	j survival[c]	a survival[d]	surv. trend[e]	pop. trend[e]	source
Netherlands	M	1959-2008	D	0.23	0.75	j +, a 0	-	1
Netherlands	M	1959-2008	D	0.33	0.75	j nb season	-	1
Netherlands Friesland	M	2000-2006	L		0.76		-	2
Great Britain	M	1963-2002	D	0.59	0.78			3
Great Britain	M	1963-1998	D	0.63	0.82	0	-	4 & 5
Sweden Västmanland	M	1987-1994	L(r)		0.74		0	6
Great Britain	M	1963-1992	D		0.83	0		7
Great Britain	M	1930-1988	D		0.81	0	-	7
Great Britain	M	1930-1988	D	0.6	0.71	a +, j 0	-	8
Denmark	M	1920-1978	D(Lack)	0.56	0.67			9
Great Britain	M	<=1952	D(Haldane?)	0.58	0.66			10
Europe	M	<=1938	D(Lack)	0.6	0.6			11

Abbreviations: see appendix A.

Literature:

1) Bruinzeel et al. 2009, 2) Schekkerman & de groep RAS Ljip 2007, 3) Sharpe et al. 2008, 4) King et al. 2008, 5) Besbeas et al. 2002, 6) Berg et al. 2002, 7) Catchpole et al. 1999, 8) Peach et al. 1994, 9) Bak & Ettrup 1982, 10) Haldane 1955 in (Boyd 1962), 11) Kraak et al. 1940

Appendix C

Adult (a) and juvenile (j, first year) survival estimates of Black-tailed Godwit.

country	habitat[a]	period	method[b]	j survival[c]	a survival[d]	surv. trend[e]	pop. trend[e]	source
Netherlands	M	1959-2008	L+D		0.7 in 1960-1970 0.8 in 1970-2008	+	-	1
Netherlands Workumerwaard	M	2004-2008	L		0.95	0	0	2
Netherlands Blokland, Zeevang, Delfstrahuizen, Schipluiden	M	2002-2005	L+D		0.93 in Zeevang, 0.81 in other sites	0	-? in Blokland, 0 in other sites	3
Iceland	M	1995-2000	L		0.87-0.94		+	4
Netherlands	M	1960-2000	D	0.36	0.77	a -? in 1995-2000, j 0	-	5
Netherlands Schaalsmeer	M	1984-1987	L(r)	0.19 (1st & 2nd yr)	0.81		-	6
Netherlands	M	1974-1980	D	0.4	0.8		-	7
Netherlands	M	? (< 1977)	?	0.624	0.68 (2nd cy), 0.63 (>2nd cy)			8
Netherlands, Denmark, other	M	<= 1952	D(Lack)	?0.70	0.70			9

Abbreviations: see appendix A

Literature:

1) Bruinzeel et al. 2009, 2) Schroeder 2010, 3) Roodbergen et al. 2008, 4) Gill et al. 2001, 5) Van Noordwijk & Thomson 2008, 6) Groen & Hemerik 2002, 7) Beintema & Drost 1986, 8) Glutz von Blotzheim et al. 1984, 9) Boyd 1962

Appendix D

Adult (a) and juvenile (j, first year) survival estimates of Curlew.

country	habitat[a]	period	method[b]	j survival[c]	a survival[d]	surv. trend[e]	pop. trend[e]	source
Sweden Västmanland	M&A	1985-1992	L(r)		0.82	0	+	1
Germany Nordrhein Westfalen	M	1973-1980	L(r)		0.89		-	2
Germany, Sweden, Finland, N-Ireland	M&?	2-6 yrs, <1992	L(r)		0.82-0.88			3
Great Britain, Ireland		1909-1975	D(Lack)	0.47	0.63 (2nd cy), 0.74 (>2nd cy)			4
Netherlands		1969-1974	D(Lack)	0.34	0.72			5
Great Britain, Sweden, others		<1950	D(Lack)	0.38	0.33 (2nd cy), 0.75 (>2nd cy)			6

Abbreviations: see appendix A.

Literature:

1) Berg 1994, 2) Kipp 1982, 3) Kipp, 1982; Ylimaunu et al. 1987, Berg, 1994 and Grant unpubl. data in (Grant et al. 1999), 4) Bainbridge & Minton 1978, 5) Speek in (Glutz von Blotzheim et al. 1984), 6) Boyd 1962

Appendix E

Adult (a) and juvenile (j, first year) survival estimates of Redshank.

country	habitat[a]	period	method[b]	j survival[c]	a survival[d]	surv. trend[e]	pop. trend[e]	source
Netherlands	C+M	1959-2008	D	0.53	0.76	0	-	1
Sweden - Gotland	M	1997-2003	L		0.80	0	0	2
England - Cardiff Bay	C	1997-2003	L		0.85 (<1999 pre-closure), 0.78 (>1999 post-closure)	- (>1999)	- (>1999)	3
England - Rhymney Estuary	C	1991-2003	L		0.86	0	+ (>1999)	3
Wales - Severn Estuary	C	1988-2003	L		0.73 (<1999), 0.93 (>1999)	+ (>1999)		3
England - Cardiff Bay	C	1990-1999	L		0.88			3
Scotland - Moray Firth	C	1978-1994	L		0.43 (2nd cy), 0.67 (3rd cy), 0.74 (>3rd cy)	0	0	4
Wales - Nortern Wales		1983-1984	L(?)		0.82			5
England - Northwest England	C	1974-1984	L		0.72 (f), 0.75 (m)	0	+ (1978-1982), - (1982-1985)	6
Scotland - South Uist	C	1985-1988	L(r)		0.75 (f), 0.77 (m)			7
Sweden		<= 1958	D(Lack)	0.45	0.69			8
Germany - Wangerooge	C	1955-1957	L(r)		0.75		+	9
Germany - Wangerooge	C	1955-1957	D(Lack)		0.56		+	9
Germany - Wangerooge		1955-1957	L(r)		0.70		+	10

Abbreviations: see appendix A.

Literature:

1) Bruinzeel et al. 2009, 2) Ottvall 2005, 3) Burton et al. 2006, 4) Insley et al. 1997, 5) Moss, 1985, in (Burton 2000), 6) Thompson & Hale 1993, 7) Jackson, 1988 in (Burton 2000), 8) Boyd 1962, 9) Grosskopf 1964, 10) Grosskopf 1959

7 General discussion

Introduction

Overview of thesis

Many sites in The Netherlands are polluted, amongst which agricultural grasslands harbouring breeding populations of Black-tailed Godwits (*Limosa limosa*, ssp. *limosa*), a species classified 'vulnerable' on the IUCN and the Dutch Red list. The initial research aim of this thesis was therefore to answer the question "What are the population level effects of diffuse pollution, in the form of heavy metals, on Black-tailed Godwits breeding on contaminated soils in The Netherlands?". For this purpose heavy metal concentrations were measured in soil, earthworms, godwit eggs and feathers, and population studies were conducted at a polluted (Blokland) and a reference site (Zeevang). We found higher concentrations of Lead, Mercury and Cadmium in godwits at the polluted site, even though soil concentrations were all below Dutch intervention values and the species spends only a few months of the year in the breeding area (Roodbergen *et al.* 2008b, Chapter 2). However, neither nest success nor the number of eggs hatched per successful nest differed between the two sites, whereas the maximum estimate for chick survival was significantly higher in the polluted site (Blokland). Chick survival decreased with increasing hatching date. Total reproductive output in the two sites was lower than found in previous studies, and in most years reproductive output was too low to compensate for adult and juvenile mortality (Roodbergen & Klok, 2008, Chapter 3). Adult survival in Blokland was lower than in Zeevang, but equal to two other non-contaminated sites (Schipluiden and Delfstrahuizen), suggesting no effects on local adult survival. Moreover, estimates were similar to those from the 1970s and 1980s indicating that it is unlikely that the present population decline in The Netherlands is caused by changes in adult survival (Roodbergen *et al.* 2008a, Chapter 4).

As it proved difficult to find effects of heavy metals on vital rates of the Black-tailed Godwit population at the contaminated site, the focus of the project was shifted towards population dynamics of Black-tailed Godwits and other meadow breeding waders. Insight into population dynamics of a vulnerable species is essential for effective conservation (Caswell, 2001). Therefore, in Chapter 5 (Klok *et al.* 2009), we extended an existing modelling framework, to diagnose the population decline in five meadow-breeding waders; Black-tailed Godwit, Curlew (*Numenius arquata*), Lapwing (*Vanellus vanellus*), Oystercatcher (*Haematopus ostralegus*), and Redshank (*Tringa totanus*). The framework was based on a Leslie matrix model with three parameters: reproduction, pre-adult and adult survival. In general, adult survival had the highest elasticity, but elasticity of pre-adult survival increased with time to first reproduction, while elasticity of reproduction decreased. In all five species we advice that conservation should focus on reproduction, and in Black-tailed Godwit and Oystercatcher also on pre-adult survival. For the Lapwing populations all demographic parameters should be targeted. In Chapter 6 we summarize available

data on nest success, chick survival and reproductive output, and adult and juvenile survival of these five species in Europe. The assembled studies on survival did not show an overall decline in adult survival in any of these species. However, our meta-analyses on reproduction data show that chick survival declined strongly in the last 40 years in western Europe, while nest success declined in eastern Europe (1995-2005), in Scandinavia (1985-2005), and initially in western Europe (1950-1980). Predation rates of nests have increased by *c.* +40% in all five species in western Europe during the last four decades. Results on reproductive output (number of fledglings produced per breeding pair) were less clear-cut, possibly due to large estimate errors and a bias in the methodology. In all five species the results indicate that present population declines are caused by a decrease in reproduction, not in adult survival.

Chapter overview

In the rest of this chapter I will first discuss the results of the field study at the polluted site (Blokland) and the reference site (Zeevang), as presented in the first three chapters of this thesis. Then I will complement and integrate these results by calculating the population growth rates at the two sites and the elasticities of the population parameters, using a matrix population model developed for the Black-tailed Godwit. Most stress factors, including pollution, cannot readily be quantified, but they are likely to influence some demographic parameters more than others. Their effects on population growth rate can therefore be estimated qualitatively using elasticity analysis, putting the possible risk of pollution in a broader perspective. Next I will determine what part of the Dutch breeding population is at risk of heavy metal contamination and discuss the risks of heavy metal pollution to Black-tailed Godwits in the future. Finally, I will give recommendations for conservation of the species and discuss these in the light of heavy metal pollution.

Heavy metals and Black-tailed Godwits at polluted study site

In polder Blokland, measured soil concentrations of heavy metals were all below Dutch intervention values, but Copper (Cu), Mercury (Hg), Lead (Pb) and Zinc (Zn) were above target values indicating slightly contaminated soils (Roodbergen *et al.* 2008b, Chapter 2).

Dirven-Van Breemen *et al.* (2007) give values for Maximum Permissible Concentrations (MPCs) for secondary poisoning by heavy metals. MPCs are based on concentrations at which 5% of species are potentially affected (see Box 1) and include background ('natural') concentrations of heavy metals. The derivation of Dutch MPC values for heavy metals is described by Crommentuijn *et al.* (2000).

MPC values for the polluted site Blokland were corrected for site specific soil (lutum 23.7%, organic matter 25%, Klok *et al.* 2006) and are given in table 1, together with

Box 1. Species Sensitivity Distributions

A Species Sensitivity Distribution (SSD) is a statistical distribution function describing the variation within a sample of species in sensitivity to a specific contaminant. The basic assumption is that the sensitivities of a set of species can be described by a distribution function, which is parameterized by available toxicological data. The function describes the relationship between (log-transformed) concentrations of the contaminant and the fraction of species under consideration for which the toxicity value, e.g. the LC50 (concentration lethal to 50% of individuals of the experimental group, a value used in acute toxicity tests) or the NOEC (no observed effect concentration, used in chronic toxicity tests) will be exceeded. A SSD can be used to set an environmental quality criterion (EQC), or for ecological risk assessment (ERA). A commonly used cut-off value is the concentration at which 5% of the species is (potentially) affected, the HC5 (hazardous concentration for 5% of the species). When the concentration of a contaminant is known, the associated potentially affected fraction of species (PAF) can be estimated from the SSD (Posthuma *et al.* 2002).
Maximum Permissible Concentrations values for secondary poisoning are derived from toxicological data on both prey and predator species and are therefore assumed protective for secondary poisoning of the predator (Dirven-Van Breemen *et al.* 2007).

local soil concentrations. In Blokland, both Hg and Pb were above MPC values, while soil concentrations of Cu, Hg, Pb and Zn were elevated as compared to Zeevang (Roodbergen *et al.* 2008b, Chapter 2).

Levels of Hg and Pb in eggs and of Cd and Pb in feathers of adult Black-tailed Godwits were also significantly higher in Blokland than in Zeevang (Roodbergen *et al.* 2008b, Chapter 2). Zn and Cu, though elevated in Blokland soil and earthworms, were below local MPC values and were not transferred to eggs or feathers, probably because these elements are essential in most organisms and therefore the uptake is regulated (Eisler, 1993; Eisler, 1998).

According to Klok et al (2006), the polluted soil in Blokland can sustain lower densities of Black-tailed Godwits. In bioassays with soil from Blokland they found that earthworm biomass production was lower, and development of earthworms was retarded, resulting in a less profitable size class distribution. However, neither we (Roodbergen *et al.* 2008b, Chapter 2), nor Klok et al (2006) found significant differences in earthworm densities or biomass in the field, while Klok and Thissen (2009) even found higher densities and biomass at the polluted site. The latter

Table 1. Soil concentrations (in mg/kg) of five heavy metals in Blokland (Roodbergen et al. 2008b, Chapter 2), together with soil specific Maximum Permissible Concentration (MPC, given by Dirven-van Breemen et al. (2007) and corrected for soil characteristics at Blokland).

Heavy metal	MPC	Soil concentration
Cd	1.0	0.9
Cu	79.8	77.6
Hg	0.3	1.8
Pb	121.9	335.7
Zn	203.9	185.4

authors hypothesize this is caused by higher predation rates by higher densities of meadow birds at the reference site, but more research is needed to exclude other possibilities. If slower maturation due to heavy metal contamination retards the peak in earthworm biomass, as suggested by these authors, this could influence chick survival by affecting breeding phenology of Black-tailed Godwits at the polluted site. Högstedt (1974) found Lapwings to start laying earlier at territories with higher earthworm biomass. If earthworm densities peak later in the season at the polluted site, this could retard local laying dates. Indeed, median laying date in Blokland was significantly later compared to that in Zeevang, though only by three days. The difference between median hatching dates was larger, 11 days, but was not significant, probably due to smaller sample sizes. Delayed hatching dates can depress reproductive output, as chicks hatching later in the season have lower survival rates (Roodbergen & Klok, 2008, Chapter 3). Moreover, in Black-necked Stilts and American Avocets, Hg concentrations in down of chicks increased by 81% during the 60-day nesting season (Ackerman *et al.* 2008). Such an increase in heavy metal burdens could cause or amplify negative effects of late hatching dates on chick survival. Though effects of increased Hg concentrations were small (≤3% over a period of 28 days) compared to other factors influencing chick survival (Ackerman *et al.* 2008), they may be important when chick survival is already low.

Given the above it is worthwhile to reanalyse the data from Roodbergen & Klok (2008, Chapter 3) and Roodbergen *et al.* (2008b, Chapter 2), to see whether the seasonal decrease in chick survival is related to a seasonal increase in heavy metal concentrations in eggs. In Roodbergen & Klok (2008), the relation between hatching date and chick survival was based on data from both sites. When including an interaction between site and date, this term improved the model only for the maximum estimate of chick survival ($n=80$, $p<0.05$). The negative effect of date on the maximum estimate of chick survival, though present in both sites, was stronger in Blokland than in Zeevang. When analysing the data from the two sites separately, date significantly explained the minimum ($p<0.01$) and maximum ($p<0.001$) number of successful pairs and the maximum estimate for chick survival ($p<0.001$)

in Blokland, but not in Zeevang, though sample size was bigger at the latter site (n=44 in Zeevang vs. n=36 in Blokland). The relationship therefore seems indeed stronger in the polluted site. This could hint at effects of increasing levels of heavy metals in eggs with laying date, as found by Ackerman *et al.* (2008). These authors suggest that adult dietary exposure to Mercury may have increased over the course of the breeding season if methylation rates increased, as Mercury is only taken up in the form of methylmercury. This form is highly toxic and readily bioaccumulates in exposed organisms and biomagnifies in high concentrations in food webs (Wiener *et al.* 2003). The increase in methylation rates may be caused by rising ambient temperatures, decreasing dissolved oxygen, and anoxic conditions common during summer (Ackerman *et al.* 2008). Though Hg concentrations in godwit feathers, primarily in the form of methylmercury, were not elevated in Blokland, they were indeed elevated in godwit eggs, as were Pb concentrations (Roodbergen *et al.* 2008b, Chapter 2). However, laying date did not significantly improve models explaining log-transformed Hg or Pb concentrations in eggs (GLM in Genstat with log-transformed concentrations as dependent variables and year, site and laying date and their interactions as explanatory variables, concentrations pooled over nests, n=29, $p>0.05$). In addition, no evidence for higher frequencies of embryo malformations was found in unhatched eggs from the polluted site (unpublished data).

Though we did not find any clear effects of heavy metals at the polluted site on reproduction or adult survival, we cannot exclude that elevated levels of heavy metals in Blokland affect the local godwit population, especially as we were not able to estimate post-fledging survival. The post-fledging state could also be a sensitive period for chick survival, as heavy metal burdens may begin to increase as feather and mass growth slow at the time of fledging (Fournier *et al.* 2002; Kenow *et al.* 2003). We can only conclude that if effects on reproduction and/or adult survival are present, these are overshadowed by other factors affecting reproduction and survival.

There have been many studies on the effects of pollution from heavy metals on reproduction and/or survival in different species (e.g. Janssens *et al.* 2003; Dauwe *et al.* 2005; Eeva *et al.* 2006), but only few have linked heavy metal concentrations in diet, eggs or feathers to effects on vital rates quantitatively. A summary of possible effects of Hg, Pb and Cd is given in Box 2.

Concentrations of Pb and Hg in godwit feathers and eggs in Blokland remained below values known to cause adverse effects (Burger & Eichhorst, 2007). However, levels of Cd in earthworms in Blokland (4.27 ppm dry weight, Roodbergen *et al.* 2008b, Chapter 2) were higher than those in the diet of American Black Duck ducklings (*Anas rubripes*, 4 ppm), which caused altered behaviour in the form of hyper-responsiveness (Heinz and Haseltine 1983 in Eisler, 1985). We did not observe any effects of Cd poisoning, but symptoms of heavy metal poisoning may be very subtle (e.g. Heinz, 1979; Eeva *et al.* 2006) and therefore hard to detect. Furthermore,

Box 2. Effects of heavy metals
(summary from Gochfeld & Burger, 2001)

Lead affects all body systems and young animals are more sensitive than older animals. In vertebrates, lead poisoning can be chronic or acute, and there is no "no effect" level since the lowest measurable levels affect some biological systems. Lead exposure can cause direct mortality, as well as sublethal effects. Symptoms of lead poisoning include drooped wings, loss of appetite, lethargy, weakness, tremors, impaired locomotion, balance and depth perception, and other neurobehavioral effects. Lead affects a wide range of behaviors, including begging, feeding, growth, and cognitive abilities, which in turn affect survival in nature.
Mercury has no known metabolic function and causes a wide range of teratogenic and mutagenic effects, as well as causing embryocidal, cytochemical, histopathological, and behavioral effects. Unlike other metals, mercury both bioconcentrates and is bioamplified through the food chain. In laboratory experiments, mercury causes a wide range of reproductive effects, including lowered egg weight and shell-less eggs, embryo malformations, reduced hatchability, reduced growth, altered behavior and reduced chick survival, as well as neural shrinkage, neural lesions, and demyelination and sterility. The levels associated with these effects are 5 to 65 ppm (dry weight) in feathers, and 1 to 5 ppm dry weight (0.05 to 5.53 ppm wet weight in different species) in eggs.
Cadmium causes effects at lower concentrations than mercury or lead. In vertebrates it is carcinogenic and causes kidney toxicity, altered behavior, suppression of egg production, egg-shell thinning and testicular damage.
Effects of Copper and Zinc are not discussed, possibly because these heavy metals are regulated in most organisms (Eisler, 1993; Eisler, 1998).

effects of heavy metals are often species specific (Eeva & Lehikoinen, 1996; Dauwe *et al.* 2005). Janssens *et al.* (2003) reported significant effects of heavy metal pollution on hatching, fledging and overall breeding success in Great Tits, while Dauwe *et al.* (2005) did not find any such effects in Blue Tits at the same pollution gradient. These results suggest that even closely related species may differ considerably in their sensitivity to the direct and/or indirect effects of heavy metal pollution. Therefore, results from one species cannot readily be extrapolated to other species.

Population growth rates and elasticities of vital rates

Changes in vital rates due to heavy metal pollution, but also other factors such as intensification of agriculture or predation, need to be studied in the light of their effects on population growth rates. Therefore in this paragraph, data on reproduction and survival from Chapters 3 and 4 are integrated in a population model. With this model an elasticity analysis is performed. Elasticity analyses can be used to predict the change in population growth rate (λ) as a result to proportional changes in vital rates (Caswell, 2001). For instance, an elasticity value of 0.1 means that if a vital rate is increased by 5%, population growth rate will increase by 0.5% (0.1x5%).

The matrix population model used here is similar to the models described in Chapter 5 (Klok *et al.* 2009) of this thesis, with the exception that pre-adult survival is divided into post-fledging juvenile survival and 2nd year survival. Similarly to Schroeder *et al.* (2009), survival in the second year is assumed to be equal to adult survival, as in *islandica* juvenile survival after autumn migration is high (pers. comm. J. Gill). This means that the matrix can be simplified to a 2 x 2 matrix. However, we assume that first year, post-fledging survival is equal to 0.6, in stead of 0.4 as assumed by Schroeder *et al.* (2009). Van Noordwijk and Thomson (2008) give a value for first year survival of 0.4, but this value includes part of pre-fledging mortality; post-fledging survival will therefore be higher. In addition, the assumption that all individuals breed is released (see Schroeder *et al.* 2009), and reproductive output is separated into different components, using the formula given by Schekkerman & Muskens (2000). In contrast with Schroeder *et al.* (2009), we assume that maximum lifespan is 30 years (Zwarts *et al.* 2009) and that Black-tailed Godwits start to breed in their third calendar year, as the proportion breeding in their second calendar year is small (Cramp & Simmons, 1983). The population model is described in more detail in Box 3 and the calculation of elasticity values of vital rates in Box 4. Matrix elements and vital rates for Blokland, Zeevang and the two sites combined are given in table 2, together with the (combined) elasticity values and resulting population growth rates (λ).

In both sites, the godwit population is declining; in Blokland more rapidly (9% per year, λ=0.91) than in Zeevang (2% per year, λ=0.98). This difference is mainly caused by the difference in local adult survival rates, which may include dispersal to other sites. For the two sites combined, population growth rate is calculated to be 0.92, which means the combined population is decreasing by 8% per year, somewhat faster than the 5% overall average Dutch yearly decrease given by Teunissen & Soldaat (2006).

It is clear that in these two populations, population growth rate is most sensitive to the vital rate adult survival (elasticity: 0.83). This is a general result found in long-lived species (a.o. Heppell *et al.* 2000; Stahl & Oli, 2006; Klok *et al.* 2009, Chapter 5). Next come 1st year (post-fledging) survival, proportion breeding, hatching success

Table 2. Values for vital rates and matrix elements used in the matrix population model (Box 3) per site and combined, their elasticity values (combined) and their source, together with the resulting population growth rates. B=Blokland, Z=Zeevang.

	Symbol	Value			Elasticity	Source
		B	Z	B+Z	B+Z	
Matrix elements						
Reproductive output per 1st yr (2nd cy) female	F1	0	0	0	0	Assumption (see Cramp & Simmons, 1983)
1st yr (post-fledging) survival	G1	0.6	0.6	0.6	0.09	Assumption
Reproductive output per adult female	F2	0.16	0.10	0.14	0.09	Calculated from lower-level parameters b, n, h, c, r and s
Adult survival, including maximum life-span	P2	0.81	0.92	0.82	0.81	Calculated from lower-level parameters s and d
Vital rates						
1st yr (post-fledging) survival	G1	0.6	0.6	0.6	0.09	Assumption
Adult survival	s	0.81	0.93	0.83	0.83	(Roodbergen *et al.* 2008a, Chapter 4)
Duration adult stage	d	29	29	29	0.02	Max age recorded is 30 yrs (Zwarts *et al.* 2009)
Proportion breeding	b	0.8	0.8	0.8	0.09	Assumption (see Schroeder *et al.* 2009: 0.5-0.89)
Nest success	n	0.37	0.43	0.39	0.08	(Roodbergen & Klok, 2008, Chapter 3)
Clutch size (# eggs hatched per successful nest)	h	3.33	3.50	3.46	0.09	(Roodbergen & Klok, 2008, Chapter 3)
Chick survival	c	0.30	0.14	0.24	0.09	(Roodbergen & Klok, 2008, Chapter 3)
Probability of replacement clutch after nest failure	r	0.5	0.5	0.5	0.05	Assumption (see Schekkerman & Müskens, 2000)
Population Growth Rate	λ	0.91	0.98	0.92		

Box 3. Matrix population model

In the matrix model, only females are explicitly taken into account, and it is assumed that (i) the sex ratio is 1:1, (ii) the population growth rate is independent of density, (iii) the survival of females is equal to that of males and (iv) breeding takes place in a short period ('pulse') in spring. We censused the modeled population yearly just after juveniles have fledged (post-breeding).

The resulting matrix describing the population dynamics in Black-tailed Godwits has the form:

$$A := \begin{pmatrix} F1 & F2 \\ G1 & P2 \end{pmatrix}$$

with
$F1 := 0$
$G1 := 0.6$

$$F2 := b \cdot s \cdot [0.5 \cdot [\, 1 + r \cdot (1 - n)\,] \cdot n \cdot h \cdot c]$$

$$P2 := s \cdot \left[1 - \frac{\left(\frac{s}{\lambda}\right)^{d} - \left(\frac{s}{\lambda}\right)^{(d-1)}}{\left(\frac{s}{\lambda}\right)^{d} - 1} \right]$$

Here, F1 is the number of fledglings produced per first year female, which is assumed to equal zero. G1 is juvenile, post-fledging survival. P2 is calculated using the duration of the adult stage, adult survival and λ, which is calculated using an iterative function (where λ is being calculated by iteration until it remains constant, Heppell *et al.* 1994). F2 is the number of fledglings produced per adult (≥3rd cy) female and is calculated using the formula for reproductive output from Schekkerman & Müskens (2000) and data from Roodbergen & Klok (2008, Chapter 3). The resulting reproductive output per breeding pair is divided by 2, as only the females are included, and multiplied by the proportion breeding and by adult survival, as the female first needs to survive before she can start breeding (post-breeding census).

Box 4. Calculating elasticities of matrix elements and vital rates.

The sensitivities of the matrix elements $a_{i,j}$ can be calculated by using the right (w) and left (v) eigenvectors for the dominant eigenvalue of the matrix (Caswell, 2001):

$$\frac{\delta\lambda}{\delta a_{i,j}} := \frac{(v_i \cdot w_j)}{(|v \cdot w|)}$$

These eigenvectors have biological meaning; the right eigenvector w represents the stable age distribution, i.e. the composition of the population in age classes that the population can attain in the long run. The left eigenvector v gives the reproductive values, i.e. the expected relative reproductive output of the different age classes.
The elasticities $e_{i,j}$ of the matrix elements can be calculated from the sensitivities using:

$$e_{i,j} := \frac{a_{i,j}}{\lambda} \cdot \frac{\delta\lambda}{\delta a_{i,j}}$$

The elasticities of the matrix elements sum to one and can therefore be seen as the contributions of these elements to the population growth rate.
According to Caswell the elasticity of λ to a lower level parameter (vital rate) x can be calculated from:

$$\frac{x}{\lambda} \cdot \frac{\delta\lambda}{\delta x} := \frac{x}{\lambda} \cdot \sum \frac{\delta\lambda}{\delta a_{i,j}} \cdot \frac{\delta a_{i,j}}{\delta x}$$

The elasticities of the vital rates do not sum to one and therefore cannot be interpreted as contributions to λ, as λ is not a homogeneous function of the vital rates. These elasticities quantify the effect of a relative change in a vital rate in terms of a relative change in the population growth rate. They are valid only locally, as the relation between a vital rate and λ is usually not linear.

and chick survival (elasticities: 0.09), closely followed by nest success (elasticity: 0.08). Probability of a replacement clutch and duration of adult stage are least important (elasticities: 0.05 and 0.02 respectively). The number of fledglings per breeding pair is a parameter estimated in many studies and can be calculated from

the vital rates n, h, c and r (see Schekkerman & Müskens, 2000). In the two sites combined, this parameter equals 0.42, with an elasticity value of 0.09. Elasticity values differ for the three parameter sets (Blokland, Zeevang and combined), but the order of importance of both matrix elements and vital rates remains the same.

Adult survival is already high, has probably not decreased (Roodbergen *et al.* 2008a, Chapter 4 and Chapter 6; Bruinzeel *et al.* 2009) and is difficult to influence, which leaves little scope for improvement. Juvenile survival is also difficult to influence. Reproductive parameters (n, h, c and r), however, have decreased (Roodbergen & Klok, 2008, Chapter 3, and Chapter 6; Schekkerman *et al.* 2009) and can be influenced by proper management measures. Increasing chick survival would be most effective, as of all reproductive parameters chick survival and the number of eggs hatched per successful nest have the highest elasticity values. However, the latter is difficult to influence because godwits usually lay only four eggs. According to the model, the number of fledglings produced per breeding pair needs to increase by 102%, from 0.42 to 0.86 in order to reach a stable population (λ=1). This could be achieved by for instance increasing chick survival by 103% from 0.24 to 0.49. The population will continue to decrease if only nest success is increased, even to a nest success of 100%. The same goes for the proportion of females that attempt to breed. In their most optimistic scenario, Schroeder *et al.* (2009) calculated a required reproductive output of 0.85 fledglings per pair. Although their assumptions and model structure differ from those discussed here, the two values for required reproductive output are very similar. Clearly, such a large increase in reproductive output and underlying vital rates will be difficult to achieve. This implies that several reproductive parameters will need to be targeted at the same time, with the main focus on chick survival and nest success and the proportion breeding. The same is probably even more true for the total Dutch godwit breeding population, as adult survival based on national ringing recoveries (0.77, Van Noordwijk & Thomson, 2008; 0.8, Bruinzeel *et al.* 2009) is lower than at our two study sites.

One should keep in mind that the model is a crude simplification of reality. It is based on a limited data set, while variation in estimates of demographic parameters is high (Chapter 6). Moreover, in reality parameters are not constant, but fluctuate in time and space. Estimation error and stochasticity tend to decrease population growth rates (Tuljapurkar, 1990). Therefore in reality the necessary increase in reproductive output (and thus the underlying parameters) will even be higher.

To illustrate possible effects of heavy metals on the population growth rate by affecting different vital rates, I here assume that every vital rate would be reduced by the same factor, namely 0.95. This would result in an extra population decrease of 4.5% when adult survival is affected, 0.5% when either juvenile survival, proportion breeding, hatching rate or chick survival are affected, 0.4% when nest success is affected, and 0.1% when either maximum lifespan or the probability of laying a replacement clutch are affected.

Heavy metals may influence both survival and reproduction (see Box 2), but reproduction tends to be more sensitive, as adults can partly expose of their heavy metal burden through sequestration into feathers and eggs (Furness *et al.* 1986; Burger & Gochfeld, 1993; Burger, 1993). In addition, embryo's and chicks are generally more vulnerable to toxicants than adults (Hoffman, 2003). On the one hand this is positive, as population growth rate is less sensitive to reproductive output than to adult survival (see above). However, although the life history strategy of the Black-tailed Godwit is robust to stochastic breeding failure (a 'bet hedging' strategy; Stearns, 1999), it is sensitive to a chronic reduction of reproductive output. Contaminants such as heavy metals may remain in the food web for a long time, causing chronic exposure. This means that even though population growth rate is most sensitive to adult survival, a persistent reduction of reproductive output such as may be expected from contaminants may ultimately cause population declines (Rowe, 2008). A clear example of this is the ongoing intensification of agriculture, which caused population declines of meadow birds, through a sustained reduction in reproductive success.

Heavy metals and Black-tailed Godwits in The Netherlands

To determine what proportion of the total Dutch breeding population of Black-tailed Godwits could be affected by heavy metals, spatial data on breeding numbers of Black-tailed Godwits (Teunissen *et al.* 2005) were joined in Arcview to spatial data on soil heavy metal concentrations (Brus *et al.* 2002) and on physical geographical regions. Data on soil heavy metal concentrations were only available for the heavy metals Cd, Cu, Pb and Zn. For each heavy metal the MPC value per soil type (peat, riverine clay, marine clay, sand and loam; simplified soil classification used for physical geographical regions) was calculated, by using the correction factors for standard soil and the lutum and organic matter content of each soil type (table 3, lutum and OS contents derived from Dirven *et al.* 2002; MPC values derived from Dirven-Van Breemen *et al.* 2007).

Of the total Dutch breeding population of Black-tailed Godwits, it is estimated that *c.* 14% is confronted with levels above MPC of at least one of the four heavy metals studied (Cd, Pb, Cu, Zn in order of importance, table 4, figure 1). Of these 14%, 3% is confronted with levels above MPC of at least two and 0.4% of at least three of these heavy metals (table 4, figure 2).

The above percentages would be higher if Hg could also be included, as Hg concentrations tend to be higher in peat soils than in other soil types (Slooff *et al.* 1994) and Black-tailed Godwits prefer peat soils for breeding (36% of the Dutch godwit population breeds on peat soils which constitute only 8% of Dutch soil

Table 3. Values for Maximum Permissible Concentration per soil type, derived from Dirven-Van Breemen et al. (2007).

Heavy metal	Peat (19% lutum, 26% OM)	Riverine clay (26% lutum, 14% OM)	Marine clay (22% lutum, 14% OM)	Sand (3% lutum, 6% OM)	Loam (14% lutum, 5% OM)
Cd	0.96	0.78	0.76	0.49	0.54
Cu	75.83	70.42	66.08	36.83	47.67
Hg	0.26	0.26	0.25	0.18	0.21
Pb	117.35	111.18	106.24	72.88	85.24
Zn	187.71	191.57	176.14	87.43	127.93

types, SOVON data). Concentrations are also elevated in river floodplains, which contain 11% of the Dutch Black-tailed Godwit breeding population (SOVON data) and in polders where harbour sediment or city waste has been applied as a top layer (Slooff *et al.* 1994). In such areas values of 1-10 mg/kg Hg can be found, which are higher than MPC values for any soil type (Slooff *et al.* 1994). Moreover, during migration and wintering, but also at the breeding sites before breeding, Black-tailed Godwits make use of wetlands and flooded areas. Such areas are known as 'Hg sensitive' ecosystems, as methylation of Hg takes place at oxic-anoxic interfaces. The production of methylmercury in wetlands can increase greatly during flooding (Wiener *et al.* 2003).

Black-tailed Godwits are migratory and will only be exposed to these particular levels of heavy metals during the breeding season (*c.* 4-5 months), whereas HC5 values are based on chronic exposure. However, Black-tailed Godwits often return to the same breeding grounds (Groen, 1993; Roodbergen *et al.* 2008a) and have a long maximum lifespan, the oldest individual ever recorded in literature being 30 years of age (Zwarts *et al.* 2009). Therefore the cumulative exposure in Black-tailed Godwits on contaminated breeding grounds can be considerable.

Little is known about exact migratory routes and about risks from heavy metal contamination outside the breeding season. However, as godwits mainly use wetlands in this period, they may be exposed to higher levels of methylmercury (see above) and Pb. Levels of Pb exposure through gunshot ingestion are high in many wetlands, particularly those in the Mediterranean (Pattee & Pain, 2003).

To see whether the elevated levels of heavy metals in Dutch soils influence local population trends, study sites with known population trends of Black-tailed godwits (SOVON data) were joined to spatial data on soil heavy metal concentrations (Brus *et al.* 2002). Unfortunately, none of these sites was situated on soils with heavy metal levels above MPC and therefore effects could not be studied.

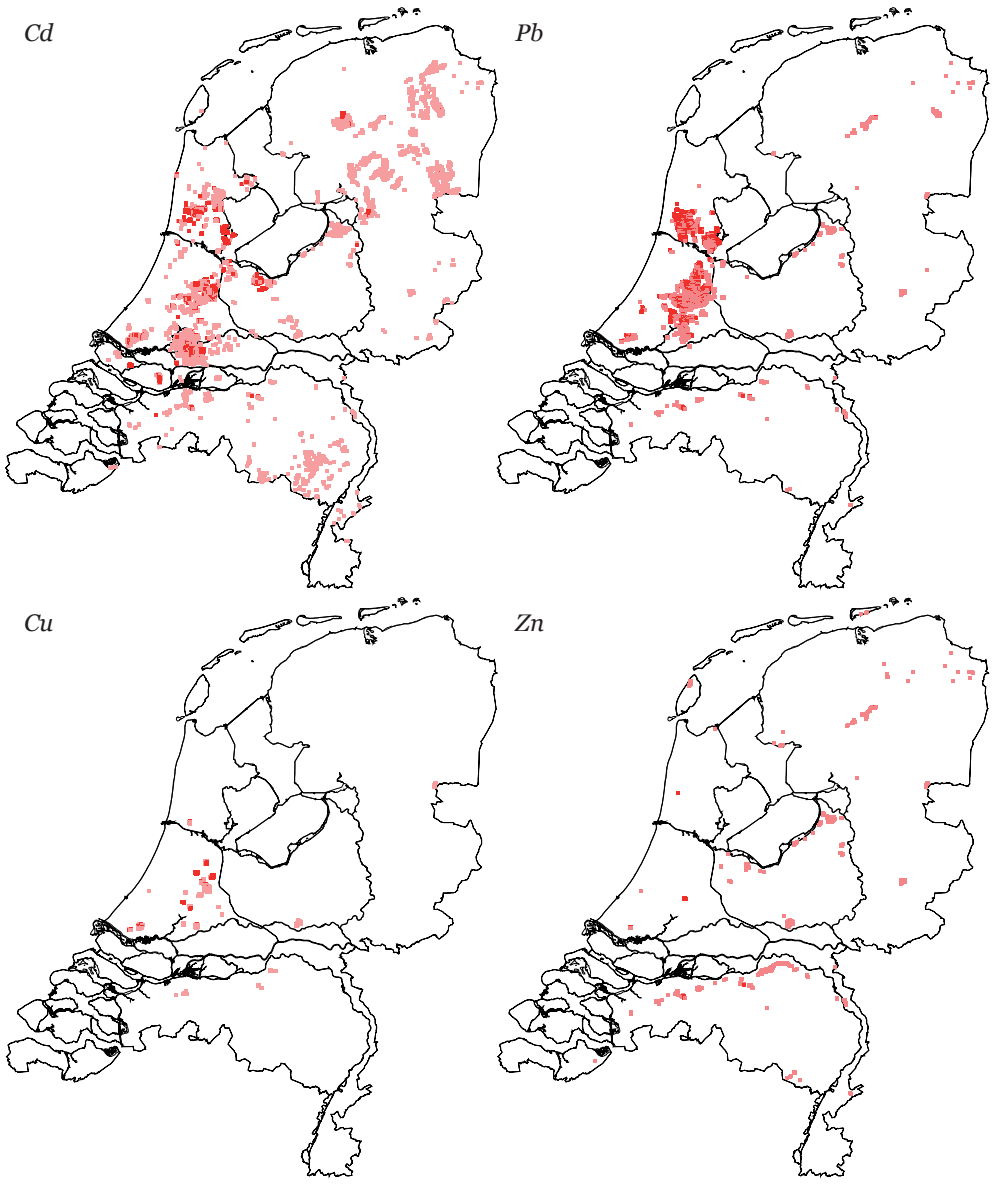

Figure 1. Breeding sites of Black-tailed Godwits at which heavy metal concentrations are above MPC. Pink: <1 breeding pair/km2, red: >1 breeding pair/km2.

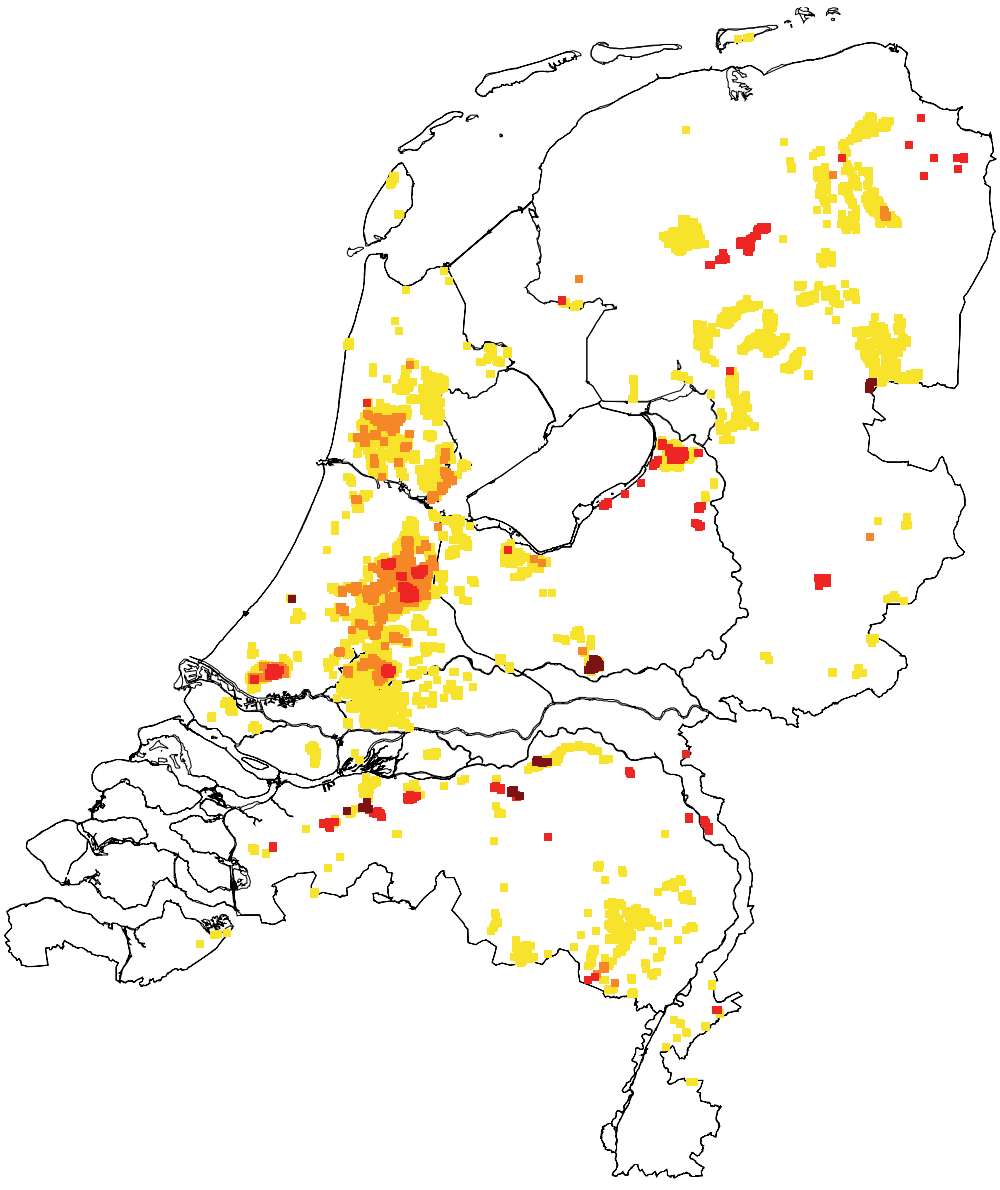

Figure 2. Breeding sites of Black-tailed Godwits at which concentrations of one (yellow) two (orange), three (red), or four (dark brown) of the heavy metals Cd, Cu, Pb and Zn are above MPC.

Table 4. Distribution of breeding pairs of Black-tailed Godwits over soils with heavy metal concentrations above the Maximum Permissible Concentration (MPC, in mg/kg). Estimated numbers of breeding pairs for the year 2004 are obtained from SOVON (Teunissen & Soldaat, 2005). Heavy metal soil concentrations are obtained from Brus et al.(2002).

Heavy metal above MPC value	Estimated no. of breeding pairs	% of population
Cd	5147	8.3
Cu	461	0.7
Hg	?	?
Pb	4560	7.3
Zn	137	0.2
≥1 heavy metal	8 523	13.7
>1 heavy metal	1 309	3.1
>2 heavy metals	235	0.4
NL	62 174	100.0

Future risks of heavy metals in The Netherlands

Although it is not likely that heavy metals are a driving factor in population declines of meadow birds, they may have additive effects on already vulnerable populations. Moreover heavy metals may pose a greater risk in the future, as concentrations of heavy metals in Dutch soils have increased and are increasing from anthropogenic sources: Cd soil concentrations have increased with 49%, Pb concentrations with 38%, Cu concentrations with 22% and Zn concentrations with 18%, as compared to natural background levels (Spijker *et al.* 2008). Again, no data are given on Hg. On Dutch dairy farms, yearly accumulation of heavy metals is considerable (table 5, Groot *et al.* 1998; Boer & Hin 2003). Boer & Hin (2003) warn that within possibly 50 years, grassland peat soils will become unsuitable for agriculture, should these input levels remain constant. Remediation will be difficult, as heavy metals bind strongly to organic soil particles.

According to Boer & Hin (2003), this accumulation is mainly caused by mixed feed and feed concentrate and artificial fertilizers. Another factor causing heavy metal concentrations to increase in peat soils is oxidation of organic matter due to lowering of the groundwater table (Rutgers *et al.* 2007). In addition, acidification of agricultural soils may increase bioaccumulation of heavy metals in earthworms (Nahmani *et al.* 2007), and thus the risks to their predators. Also in higher-level organisms, calcium (Ca) deficiency, which is more likely to occur on soils with low pH, increases heavy metal uptake, as organisms respond by increased production of Ca-binding proteins, which also bind to heavy metals (Washko & Cousins, 1977, in Silver & Nudds, 1995).

Table 5. Yearly accumulation of heavy metals on Dutch dairy farms. No data available on Hg.

Study area	Period	Cd (g/ha/yr)	Cu (g/ha/yr)	Pb (g/ha/yr)	Zn (g/ha/yr)	source
Dutch dairy farms on peat soils	1995	3	112	30	320	Groot *et al.* 1998
Dutch dairy farms	1997-2001	0.85	180	Not given	455	Boer & Hin 2003

Recommendations for management

Management agreements in The Netherlands should focus on increasing reproductive output, most effectively by increasing both chick survival and nest success, but also by increasing the proportion of birds attempting to breed (see above). Thus far, management agreements proved ineffective (Kleijn *et al.* 2001; Kleijn & Van Zuijlen, 2004) and should therefore be improved, by focusing more strongly on the needs of Black-tailed Godwits. Most meadow breeding waders, notably Black-tailed Godwit and Redshank, prefer fields with high groundwater levels for breeding (Verhulst *et al.* 2007; Kleijn *et al.* 2008). Black-tailed Godwit families with chicks prefer tall, unmown vegetations (Schekkerman & Beintema, 2007). However, when fertilizer input is high and groundwater level low, these vegetations become dense and homogeneous in the period when most chicks are present, and are probably unsuitable for foraging chicks. Management agreements in the form of postponed mowing increase chick survival (Schekkerman *et al.* 2008) and probably nest survival, but should be accompanied by specifications on fertilizer input or floral composition (Schekkerman *et al.* 2008). In addition, groundwater levels of fields with postponed mowing should be raised to make them attractive to breeding waders (Verhulst *et al.* 2007). Higher groundwater levels might also improve conditions for adult females in the pre-laying phase, and thus increase the proportion breeding.

Increasing groundwater levels in peat soils may also diminish risks of heavy metal pollution, as it will stop oxidation of organic matter, which causes heavy metal concentrations to slowly increase (Rutgers *et al.* 2007). However, in areas with high levels of Hg contamination caution is recommended, as anoxic conditions may increase methylation rates. For this same reason, in such areas even more care should be taken when inundating meadows for meadow birds, another type of management agreement. Finally, in areas with heavy metal contamination, applying Ca may decrease heavy metal exposure, by increasing pH and reducing heavy metal uptake (see above).

Conclusions

At least *ca*. 14% of the Dutch Black-tailed Godwit population breeds on soils with heavy metal concentrations above Maximum Permissible Concentrations for secondary poisoning. The population studies conducted in the contaminated site Blokland and the reference site Zeevang showed that increased concentrations of Hg, Pb and Cd in the soil of Blokland are transferred to eggs and/or feathers of Black-tailed Godwits. However, no direct effects on reproduction or adult survival at this site were visible. It is unlikely that heavy metals drive population declines of meadow birds, but they may pose a greater risk in the future, as heavy metal concentrations on dairy farms are increasing from mixed feed, feed concentrate and artificial fertilizers, and in peat soils also from oxidation of organic matter due to lowering of the groundwater table.

Though in Black-tailed Godwits adult survival is the most important vital rate in determining population growth rate, the decline in Dutch and western European populations, is most likely caused by decreased reproduction, not by a decrease in adult survival. Conservation of the species should focus on increasing several reproductive parameters, notably chick survival and nest success, and the proportion breeding, at the same time. This could be achieved by postponed mowing, in combination with reduced use of fertilizers and elevated groundwater levels. On peat soils, raising groundwater levels will also decrease oxidation rates, thus slowing the increase of heavy metal concentrations. Applying calcium to contaminated soils will decrease the uptake of heavy metals by earthworms, and therefore reduce the risk to Black-tailed Godwits. Finally, soils heavily contaminated with Hg should not be inundated, as anoxic conditions are likely to increase the uptake and toxicity of Hg.

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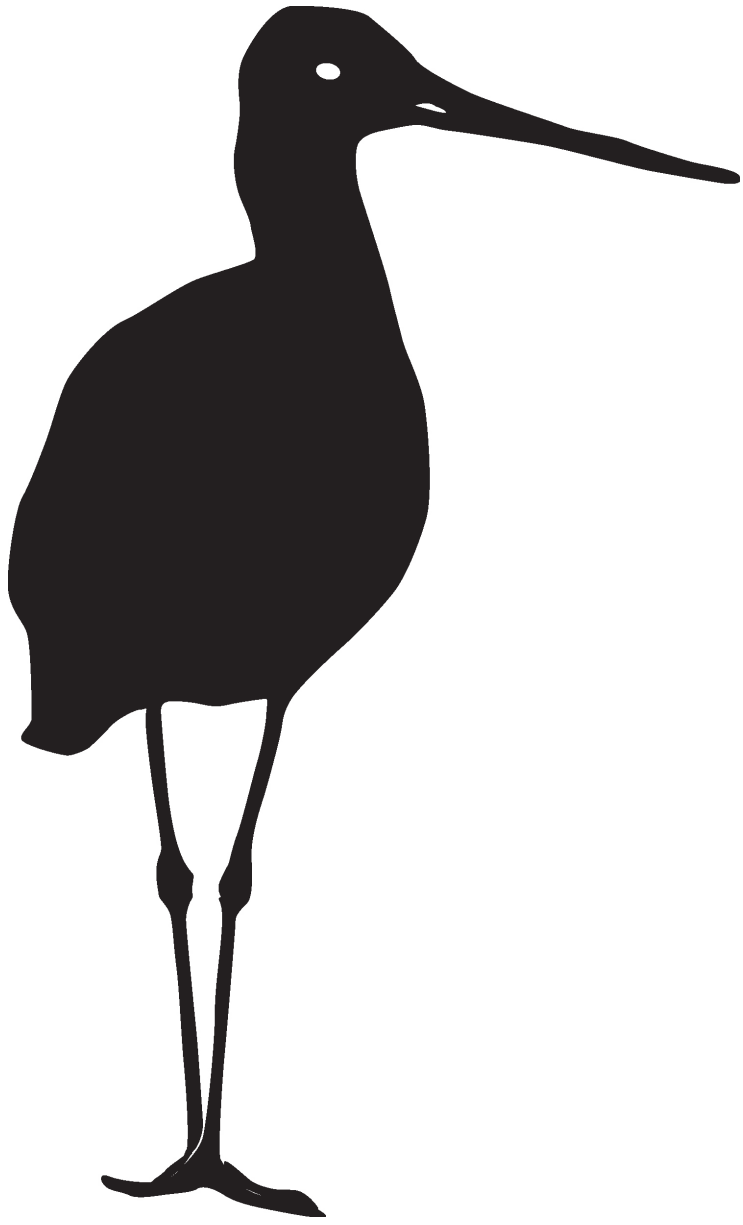
Summary



Many sites in The Netherlands are polluted. Some of these polluted sites harbour breeding populations of Black-tailed Godwits (*Limosa limosa*, ssp. *limosa*), a species classified 'vulnerable' on the IUCN and the Dutch Red list. The initial research aim of this thesis was therefore to answer the question "What are the population level effects of diffuse pollution, in the form of heavy metals, on Black-tailed Godwits breeding on contaminated soils in The Netherlands?". For this purpose heavy metal concentrations were measured in soil, earthworms, godwit eggs and feathers, and population studies were conducted at a polluted and a reference site. In the polluted site, soil concentrations of Copper, Mercury, Lead and Zinc were significantly elevated as compared to the reference site and levels of both Mercury and Lead were above Maximum Permissible Concentrations (MPC) for secondary poisoning. In earthworms, the main food item of Black-tailed Godwits before and during the breeding season, concentrations of Cadmium, Copper, Mercury, Lead and Zinc were higher in the contaminated site than in the reference site. Finally, levels of Mercury and Lead in eggs and of Cadmium and Lead in feathers of adult Black-tailed Godwits were significantly higher in the polluted site than in the reference site, even though the species spends only part of the year in the contaminated breeding area. However, neither nest success nor the number of eggs hatched per successful nest differed between the two sites, whereas the maximum estimate for chick survival was significantly higher in the polluted site. Godwits started laying three days later in the polluted site than in the reference site and chick survival decreased with increasing hatching date. Total reproductive output in the two sites was lower than found in previous studies, and in most years reproductive output was too low to compensate for adult and juvenile mortality. Adult survival in the contaminated site was lower than in the reference site, but equal to that in two other non-contaminated sites, suggesting no effects on local adult survival. Moreover, estimates were similar to those from the 1970s and 1980s indicating that it is unlikely that the present population decline in The Netherlands is caused by changes in adult survival.

As it proved difficult to find effects of heavy metals on vital rates of the Black-tailed Godwit population at the contaminated site, the focus of the project was shifted towards the dynamics of declining populations of Black-tailed Godwits and other meadow-breeding waders. Insight into population dynamics of a vulnerable species is essential for effective conservation. Therefore, we extended an existing modelling framework, to diagnose the population decline in five meadow-breeding waders; Black-tailed Godwit, Curlew (*Numenius arquata*), Lapwing (*Vanellus vanellus*), Oystercatcher (*Haematopus ostralegus*), and Redshank (*Tringa totanus*). The framework was based on a Leslie matrix model with three parameters: reproduction, pre-adult and adult survival. In general, adult survival had the highest elasticity, but elasticity of pre-adult survival increased with time to first reproduction, while elasticity of reproduction decreased. In all five species we advise that conservation

should focus on reproduction, and in Black-tailed Godwit and Oystercatcher also on pre-adult survival. For the Lapwing populations all demographic parameters should be targeted.

We summarized available data on nest success, chick survival and reproductive output (number of fledglings produced per breeding pair), and adult and juvenile survival of these five species in Europe. The assembled studies on survival did not show an overall decline in adult survival in any of these species. However, our meta-analyses on reproduction data show that chick survival declined strongly in the last 40 years in western Europe, while nest success declined in eastern Europe (1995-2005), in Scandinavia (1985-2005), and inititally in western Europe (1950-1980). Predation rates of nests have increased by *c.* +40% in all five species in western Europe during the last four decades. Results on reproductive output were less clear-cut, possibly due to large estimate errors and a bias in the methodology. In all five species the results indicate that present population declines are caused by a decrease in reproduction, not in adult survival.

In the synthesizing discussion, another matrix population model is developed for the Black-tailed Godwit and parameterised with the data on vital rates from Blokland and Zeevang. In this model reproductive output is split into several reproductive parameters. The local populations at Blokland and Zeevang decline with around 9% and 2% respectively. An elasticity analysis of the two populations combined showed that population growth rate is most sensitive to adult survival, then to 1st year (post-fledging) survival, proportion breeding, hatching success and chick survival, closely followed by nest success. Probability of a replacement clutch and duration of adult stage are least important. Reproductive output needs to increase by 102% to 0.86 fledglings per breeding pair in order to reach a stable population. Such a large increase in reproductive output will be difficult to achieve, which implies that several reproductive parameters will need to be targeted, with the main focus on chick survival, the proportion breeding and nest success.

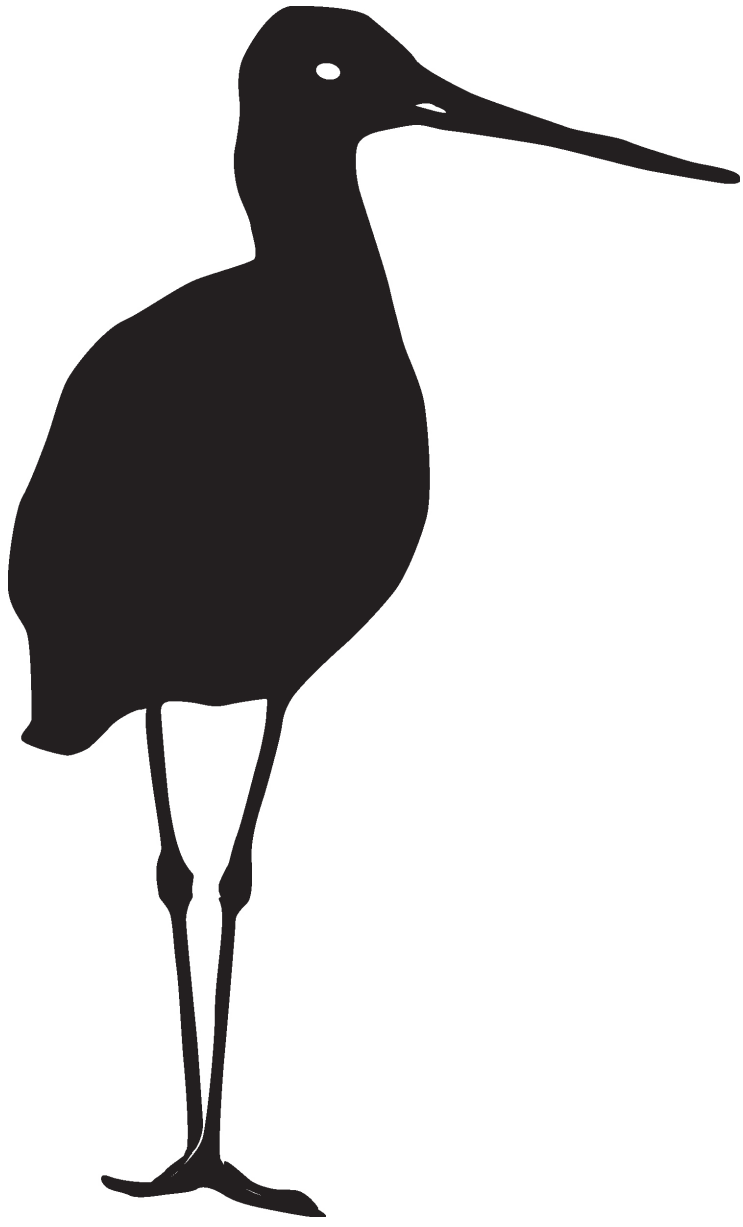
Heavy metals may influence both survival and reproduction, but reproduction tends to be more sensitive, as developing embryo's and chicks are generally more vulnerable to toxicants than adults and adults can partly expose of their heavy metal burden through sequestration into feathers and eggs. Though population growth rate is less sensitive to reproduction than to adult survival and the life history strategy of the Black-tailed Godwit is robust to stochastic breeding failure (a 'bet hedging' strategy), a persistent reduction of reproductive output such as may be expected from a chronic exposure to contaminants may ultimately cause population declines.

By joining data on breeding densities of Black-tailed Godwits to data on soil characteristics and heavy metal concentrations, I estimate that *c.* 14% of the Dutch breeding population of Black-tailed Godwits is confronted with levels above Maximum Permissible Concentrations for secondary poisoning of at least one of the

heavy metals Cadmium, Lead, Copper and Zinc. This percentage would be higher if Mercury could also be included, but no data on Mercury soil concentrations were available.

Although it is not likely that heavy metals are a driving factor in population declines of meadow birds, they may have additive effects on already vulnerable populations. Moreover heavy metals may pose a greater risk in the future, as concentrations of heavy metals in Dutch soils have increased and are increasing from anthropogenic sources. In the light of heavy metal pollution and declining meadow bird populations, we recommend that groundwater levels should be raised in fields with postponed mowing (a management agreement aimed at increasing nest and chick survival). This will make these fields more attractive to breeding waders and will improve conditions for adult females in the pre-laying phase, and may thus increase the proportion breeding. Moreover, increasing groundwater levels in peat soils may also diminish risks of heavy metal pollution, as it will stop oxidation of organic matter, which causes heavy metal concentrations to slowly increase. However, in areas with high levels of Mercury contamination caution is recommended, as anoxic conditions may increase methylation rates, increasing bioavailability and toxicity of Mercury. For this same reason, in such areas even more care should be taken when inundating meadows for meadow birds, another type of management agreement. Finally, in areas with heavy metal contamination, applying Calcium may decrease heavy metal exposure, by increasing pH and reducing heavy metal uptake.

Samenvatting



Veel gebieden in Nederland zijn vervuild, waaronder graslanden met broedende Grutto's (*Limosa limosa*, ssp. *limosa*). De Grutto staat vermeld als 'kwetsbaar' op de internationale en Nederlandse Rode Lijst. Het oorspronkelijke doel van dit onderzoek was daarom het beantwoorden van de vraag "Wat zijn de effecten van diffuse vervuiling, in de vorm van zware metalen, op de gruttopopulaties die op vervuilde grond in Nederland broeden?". Hiertoe werden de concentraties van zware metalen in bodem, regenwormen, grutto-eieren en –veren gemeten in een vervuild en een schoon referentiegebied, en werden ter plekke populatiestudies uitgevoerd. In het vervuilde gebied waren bodemconcentraties van Koper, Kwik, Lood en Zink significant verhoogd ten opzichte van de bodemconcentraties in het referentiegebied. De bodemconcentraties van Kwik en Lood overschreden bovendien de Maximum Toegestane Concentraties (MTC) voor doorvergiftiging. In regenwormen, het stapelvoedsel van Grutto's voor en tijdens het broedseizoen, waren concentraties van Cadmium, Koper, Kwik, Lood en Zink hoger in het vervuilde gebied dan in het referentiegebied. Tot slot waren concentraties Kwik en Lood in eieren en Cadmium en Lood in veren van volwassen Grutto's significant hoger in het vervuilde gebied dan in het referentiegebied, ondanks het feit dat de soort slechts een deel van het jaar in het broedgebied doorbrengt. Echter, noch het nest succes, noch het aantal eieren dat per succesvol nest uitkwam verschilde tussen de twee gebieden, terwijl de maximumschatting voor kuikenoverleving zelfs significant hoger was in het vervuilde gebied. Grutto's begonnen de eileg drie dagen later in het vervuilde gebied dan in het referentiegebied en de kuikenoverleving nam af met toenemende uitkomstdatum. De reproductive output in de twee gebieden was lager dan vermeld in eerdere studies, en in de meeste jaren was deze te laag om te compenseren voor sterfte van juveniele en volwassen Grutto's. De volwassenoverleving was in het vervuilde gebied lager dan in het referentiegebied, maar gelijk aan de overleving in twee andere niet-vervuilde gebieden, wat suggereert dat het verschil niet door de zware metalen wordt veroorzaakt. De schattingen voor de volwassenoverleving lijken op schattingen uit de jaren 1970 en 1980, wat erop wijst dat de huidige populatieafname in Nederland niet wordt veroorzaakt door een afname in de volwassenoverleving.

Omdat het moeilijk bleek effecten van zware metalen op populatieparameters van Grutto's in het vervuilde gebied aan te tonen, werd de aandacht van het onderzoek verlegd naar de dynamiek van afnemende populaties Grutto's en andere weidevogels. Inzicht in de populatiedynamiek van een kwetsbare soort is noodzakelijk voor een effectieve bescherming. Een bestaand model werd uitgebreid om de populatieafname van vijf weidevogels (Grutto, Kievit *Vanellus vanellus*, Scholekster *Haematopus ostralegus*, Wulp *Numenius arquata* en Tureluur *Tringa totanus*) te diagnosticeren. Het model was gebaseerd op een Leslie matrix model met drie parameters: reproductive output, juveniele en volwassenoverleving. Volwassenoverleving had de grootste elasticiteit, maar de elasticiteit van juveniele overleving nam toe en die van reproductive output af met toenemende leeftijd waarop voor het eerst wordt

gebroed. Bij alle vijf soorten adviseren we dat de bescherming zich moet richten op de reproductie en bij Grutto en Scholekster ook op juveniele overleving. Bij de Kievit dient bescherming zich op alle demografische parameters te richten.

We hebben beschikbare gegevens verzameld over nest succes, kuikenoverleving en reproductive ouput (aantal vliegvlugge jongen per broedpaar), en juveniele en adulte overleving van bovenstaande vijf soorten weidevogels in Europa. De gevonden studies over overleving lieten bij geen van de soorten een algemene afname in volwassen overleving zien. De meta-analyse van gegevens over reproductieve parameters toont aan dat kuikenoverleving sterk is afgenomen in west Europa in de laatste 40 jaar, terwijl nest succes is afgenomen in oost Europa (1995-2005), in Scandinavië (1985-2005), en in west Europa (1950-1980). De kans dat een nest gepredeerd wordt is toegenomen met *c.* +40% bij alle vijf soorten in west Europa in de laatste 40 jaar. Bij de reproductive output is het beeld minder duidelijk, mogelijk door grote schattingsfouten en een bias in de methode. De resultaten laten bij alle vijf soorten zien dat de recente populatieafnames worden veroorzaakt door een afname in reproductie, niet in de adultenoverleving.

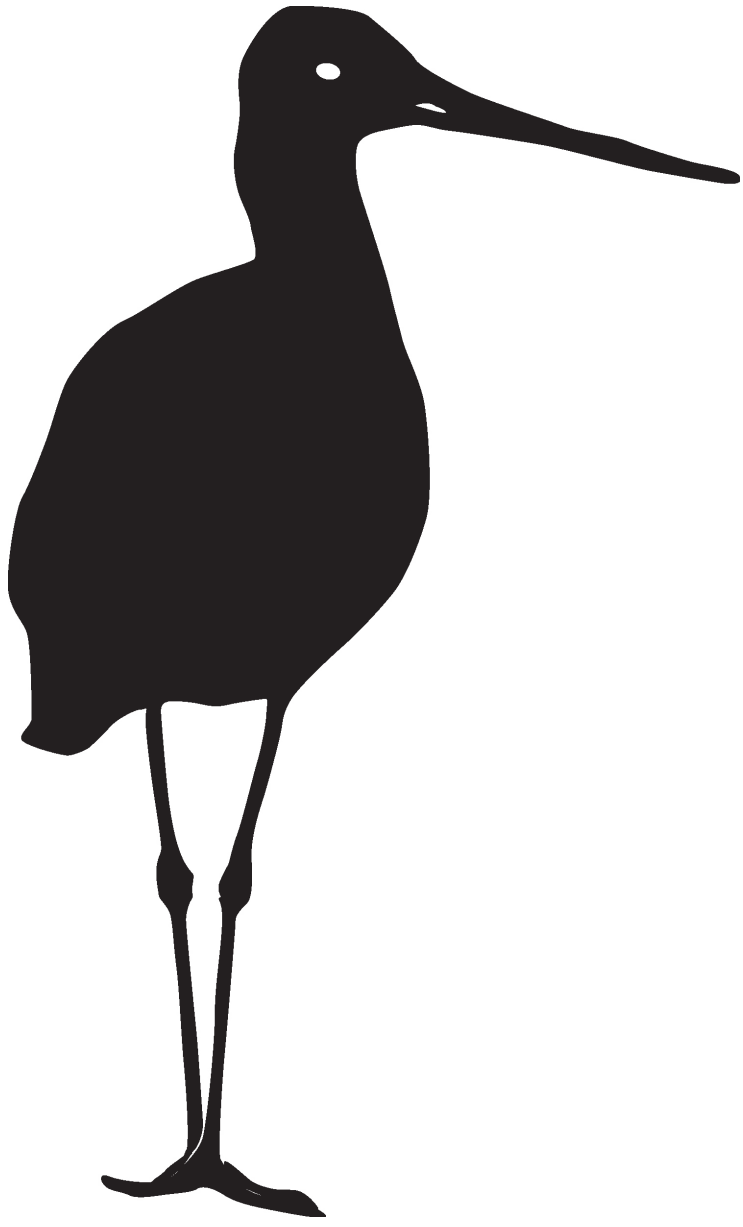
In het laatste hoofdstuk, de synthese, wordt een nieuw matrix populatiemodel ontwikkeld voor de Grutto, waarbij de totale reproductie wordt uitgesplitst in verschillende parameters. Het model wordt geparametriseerd met gegevens uit het vervuilde en het referentiegebied. De lokale populaties in deze gebieden nemen af met respectievelijk 9% en 2%. Een elasticiteitsanalyse van de gecombineerde gegevens laat zien dat de populatiegroeisnelheid het meest gevoelig is voor volwassenoverleving, dan voor eerstejaarsoverleving, het aandeel van de populatie dat gaat broeden, het aantal eieren dat uitkomt bij succesvolle nesten en kuikenoverleving, op de hielen gevolgd door nest succes. De kans op een vervolglegsel en de maximale duur van de adultenfase zijn het minst belangrijk. Voor een stabiele populatie dient de totale reproductie met 102% toe te nemen tot 0.86 vliegvlugge jongen per broedpaar. Een dergelijke grote toename in reproductie is moeilijk te realiseren, wat inhoudt dat meerdere reproductieve parameters tegelijk zullen moeten worden vergroot, waarbij de grootste inspanning moet gaan naar de kuikenoverleving, het aandeel van de populatie dat gaat broeden en het nest succes.

Zware metalen kunnen een effect hebben op zowel overleving als reproductie, maar reproductie is vaak gevoeliger, omdat zich ontwikkelende embryo's en kuikens kwetsbaarder zijn voor toxische stoffen en adulten zware metalen kunnen afscheiden via veren en eieren.. De populatiegroeisnelheid is minder gevoelig voor reproductie dan voor volwassenoverleving. Bovendien is de life history strategie van Grutto's ongevoelig voor het stochastisch mislukken van broedpogingen (een 'bet hedging' strategie). Een voortdurende reductie van de reproductive output, zoals verwacht bij een chronische blootstelling aan toxische stoffen, kan uiteindelijk toch leiden tot een populatieafname.

Door gegevens over dichtheden van broedende Grutto's te koppelen aan bodemkenmerken en concentraties zware metalen in de bodem, werd ingeschat dat *c.* 14% van de Nederlandse broedpopulatie van Grutto's wordt geconfronteerd met concentraties van minstens één van de zware metalen Cadmium, Lood, Koper en Zink die de Maximaal Toelaatbare Concentratie voor doorvergiftiging overschrijden. Dit percentage zou hoger zijn als Kwik ook in de analyse mee kon worden genomen, maar er zijn geen gegevens beschikbaar van de concentraties Kwik in de bodem.

Hoewel het onwaarschijnlijk is dat zware metalen een belangrijke rol spelen in de populatieafnames van weidevogels, kunnen ze een additief effect hebben bij populaties die reeds om andere redenen afnemen. Bovendien kunnen zware metalen een groter risico vormen in de toekomst, aangezien concentraties zware metalen in Nederlandse bodems zijn toegenomen en nog steeds toenemen door menselijk toedoen. In het licht van vervuiling met zware metalen en afnemende weidevogelpopulaties wordt aanbevolen het grondwaterpeil te verhogen op percelen met uitgesteld maaien (een beheersmaatregel gericht op het verhogen van het nest succes en de kuikenoverleving). Zo worden deze percelen aantrekkelijker gemaakt voor broedende weidevogels en worden de omstandigheden voor volwassen vrouwtjes in de fase voor de eileg verbeterd. In veenbodems kan verhogen van het grondwaterpeil bovendien de risico's van vervuiling door zware metalen verminderen, aangezien het de oxidatie van organisch materiaal voorkomt, een proces dat de concentraties van zware metalen doet toenemen. In gebieden met hoge Kwik concentraties in de bodem dient hiermee echter voorzichtig te worden omgesprongen, daar zuurstofarme omstandigheden methylatie van Kwik kunnen bevorderen, waarmee de biobeschikbaarheid en toxiciteit van Kwik worden vergroot. Om dezelfde reden dient men in dergelijke gebieden behoedzaam om te gaan met het creëren van plas-dras situaties, een ander type beheersmaatregel voor weidevogels. Tot slot kan het toevoegen van Calcium aan bodems die vervuild zijn met zware metalen de blootstelling aan zware metalen verminderen, doordat de pH wordt verhoogd en de opname van zware metalen wordt verminderd.

Acknowledgements/Dankwoord



It took a long time to write this thesis. It asked from people near to me a lot of patience and this thesis would not have been possible without their support. Writing the acknowledgements is very different from writing the other chapters, but not more easy. How to thank all the people who directly or indirectly contributed to the coming about of this thesis properly and not forget anyone?
I will give it a try!

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I promise I will do my best!

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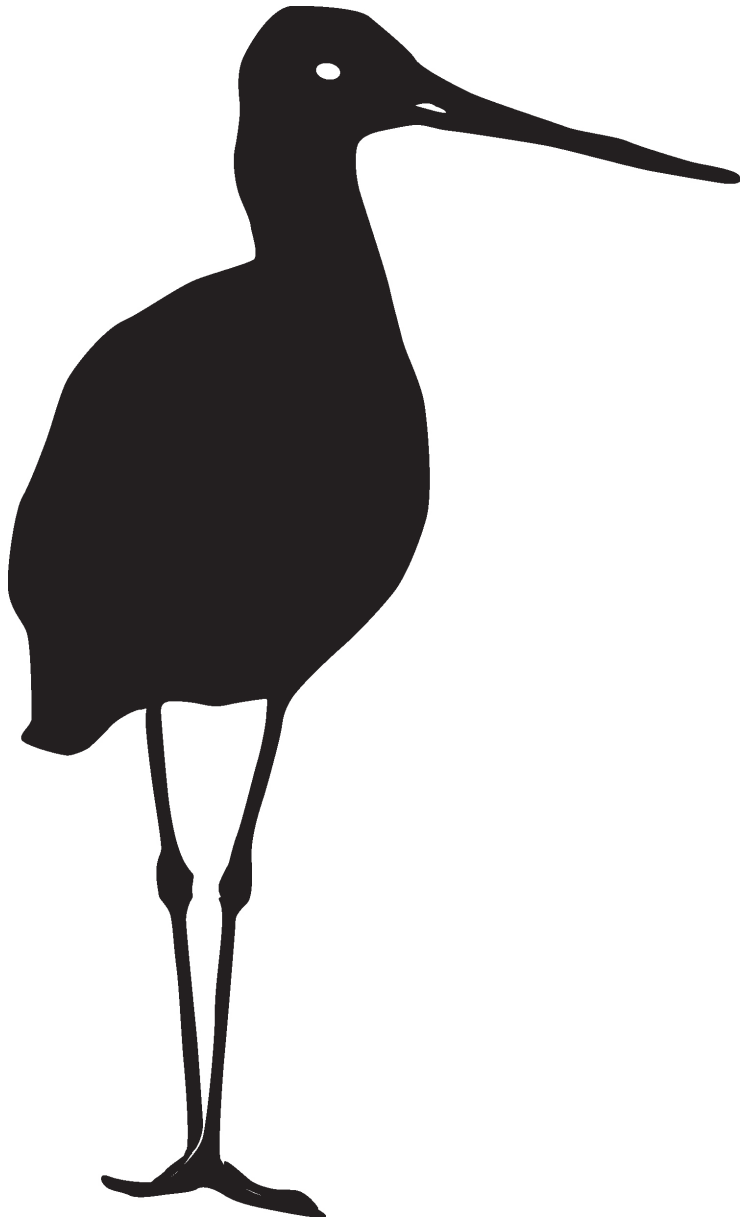

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